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Landscape Characteristics and the Occurrence of Interior Salmonids

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FINAL REPORT FOR RESEARCH AGREEMENT
#INT-96089-RJVA
"Landscape Characteristics and the Occurrence
of Interior Salmonids"
UNIVERSITY OF NEVADA-RENO
Fs Contact: Dr. Bruce Rieman
CoOp Contact: Dr. Gary Vinyard

Landscape characteristics and the occurrence of interior salmonids

Final Report

For

USDA INT-96089-RJVA

By

Jason B. Dunham

And

Gary L. Vinyard

Department of Biology and Biological Resources Research Center
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Submitted to:

Bruce E. Rieman

USDA Rocky Mountain Research Station
316 East Myrtle, Boise, ID 83702

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Introduction

This report summarizes research to explore the causes and effects of habitat fragmentation on interior salmonids. Habitat fragmentation refers to the break-up of formerly continuous habitat. This may occur naturally through processes such as succession or climate change, or through human-related disturbances, such as habitat degradation and introductions of nonnative species. Here, we report on two empirical examples of landscape-scale analyses of habitat fragmentation, and two syntheses to further explore related issues and ideas.

The first example was drawn from bull trout *Salvelinus confluentus* in the Boise River basin of south-central Idaho. This work focused on bull trout inhabiting a naturally fragmented landscape. However, the influence of human disturbance was also found to be important. This work has been accepted for publication in the Ecological Society of America's journal *Ecological Applications*, and a galley proof of this article is enclosed as part of this report.

A second example was drawn from Lahontan cutthroat trout *Oncorhynchus clarki henshawi* in the eastern Lahontan basin of southeast Oregon and northern Nevada. Previous work had implicated habitat fragmentation as an important risk factor for this threatened species. However, the causes of habitat fragmentation were not known. Furthermore, there were no available models to predict occurrence of Lahontan cutthroat trout within streams. We developed predictive models of the distribution Lahontan cutthroat trout in streams, and defined the effects nonnative species, water diversions, and channel characteristics. This work has been accepted for publication in the American Fisheries Society journal *Transactions of the American Fisheries Society*, and a copy of the accepted manuscript is enclosed.

A synthesis of this work and other related research on metapopulations, landscape characteristics, and salmonids was developed as well with Dr. Bruce Rieman (senior author) of the Rocky Mountain Research Station. This paper was accepted for publication in the journal *Ecology of Freshwater Fish*, and a copy of the revised manuscript is enclosed.

Another synthesis of ideas related to conservation assessments of inland salmonids was written and published in the Ecological Society of America's journal *Conservation Ecology*, which is available on-line, but a paper copy is included with this report.

Collectively, these works form part of a larger effort to more clearly understand the importance of landscape characteristics to interior salmonids. We have conveyed these ideas extensively through participation in regional workshops and presentations at local, national, and international meetings related to fisheries management. Our efforts to understand the importance of landscape characteristics for interior salmonids has provided critical support for developing effective conservation management and monitoring strategies.

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METAPOPULATION STRUCTURE OF BULL TROUT: INFLUENCES OF PHYSICAL, BIOTIC, AND GEOMETRICAL LANDSCAPE CHARACTERISTICS

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Abstract. Metapopulation structure of species in fragmented landscapes is ultimately the result of spatial variability in demographic processes. While specific information on demographic parameters is desirable, a more practical approach to studying metapopulations in fragmented landscapes may begin with analyses of species' occurrence in relation to large-scale habitat variability. Here, we analyzed occurrence of stream-living bull trout (*Salvelinus confluentus*) in relation to physical, biotic, and geometrical characteristics of habitats. Bull trout occurrence was analyzed at several spatial (10^x m) scales. Data were from nested sampling of 720 sites (10 m), 179 reaches (10^2 m), and 81 patches ($\geq 10^3$ m) of stream habitats within the Boise River basin of central Idaho. Based on previous findings, patches were defined as stream catchments with suitable conditions for spawning and rearing of bull trout (>1600 m elevation). Patch-scale bull trout occurrence was significantly related to patch area and isolation (stream distance between occupied patches). Lack of spatial autocorrelation between patches indicated that isolation effects were more likely the result of limited interaction among habitats (such as dispersal), rather than of correlated environmental conditions. A third factor, human disturbance in the form of roads, was associated with reduced bull trout occurrence at the patch-scale. Analyses of occurrence among reaches within occupied patches showed bull trout may select larger (>2 m width) stream habitats. Occurrence of bull trout was not associated with nonnative brook trout (*Salvelinus fontinalis*) at large (patch), intermediate (reach), or small (site) spatial scales. Definition of a metapopulation structure for bull trout in the Boise River basin was complicated by uncertainties in the frequency and magnitude of dispersal. From the distribution of patch sizes and isolation among occupied patches, we suggest the metapopulation is a complex mosaic of several elements found in conceptual models. This complexity poses a challenge to empirical and theoretical attempts to study stream-living bull trout. Future work to define the structure of bull trout metapopulations must relate temporal and spatial patterns of patch occupancy with complex patterns of dispersal that likely interact with habitat spatial structure, life history variability, and the historical context of regional climate changes. Results of this work suggest conservation of bull trout should involve protection of larger, less isolated, and less disturbed (as indexed by road densities) habitats that may serve as important refugia or sources of recolonization. Bull trout populations in smaller, isolated, and more disturbed habitats may be at risk of extinction. Finally, metapopulation structure implies the existence of suitable, but presently unoccupied habitat, which should be managed carefully to facilitate potential natural recolonization or reintroductions of bull trout.

Key words: bull trout; extinction risk; habitat fragmentation; incidence functions; landscape ecology; metapopulations; Salvelinus; *stream ecology.*

INTRODUCTION

Natural landscapes are mosaics of habitats affected by a variety of physical and biotic processes that operate on different spatial and temporal scales (Hansson et al. 1995, Wu and Loucks 1995, Collins and Glenn 1997). Accordingly, the distribution of organisms is rarely homogeneous across landscapes, and populations may be subdivided or patchy (Karieva 1990). Due to extinction of local populations and/or movements of animals across landscapes, not all suitable habitat patches will be occupied at any single point in time. Populations with these characteristics are typically described as metapopulations (Hanski and Gilpin 1996). Patterns of habitat (patch) occupancy in metapopulations are ultimately the result of spatial variation in demographic processes, namely rates of natality, mortality, immigration, and emigration (Pulliam 1988). Estimates of these population parameters are difficult to obtain (Ims 1995, Ims and Yoccoz 1996), and typically available for only one or a limited number of subpopulations, which may not represent status of the metapopulation (Middleton and Nisbet 1997). An alterna-

Manuscript received 22 September 1997; revised 25 March 1998; accepted 26 May 1998.

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tive approach to studying metapopulations is to analyze patterns of presence or absence of organisms (occurrence) in relation to landscape characteristics (Hanski 1994, Sjögren-Gulve 1994, Bolger et al. 1997). Inferences from patterns of occurrence may be subject to a variety of limitations (see Taylor 1991, Hanski et al. 1996, Sjögren-Gulve and Ray 1996), but can nonetheless provide practical insights into the structure and dynamics of metapopulations.

In this study, we investigated patterns of occurrence in stream-living bull trout (*Salvelinus confluentus*) in relation to physical, biotic, and geometrical landscape characteristics. Bull trout occupy a naturally fragmented and complex mosaic of stream habitats that may be increasingly fragmented by human-related disturbances, including introductions of nonnative fishes, habitat degradation, dams, and altered disturbance regimes (Rieman and McIntyre 1993, 1995, Rieman et al. 1997*a*). The large-scale geometry of fragmented landscapes is characterized by the size, shape, spatial distribution, and isolation of habitats (Fahrig and Merriam 1994). The interaction of these geometrical characteristics with life histories, local and regional environmental variability, and human disturbance is one of the central problems of landscape ecology and metapopulation dynamics (Wiens 1996). Increasingly, studies of stream-living salmonids (such as bull trout) are revealing important patterns and processes at large ($\geq 10^3$ m) spatial scales that may not be apparent at smaller ($10-10^2$ m) spatial scales (e.g., Fausch et al. 1994, Rieman and McIntyre 1995, 1996, Keleher and Rahel 1996, Dunham and Vinyard 1997, Wiley et al. 1997).

Previously, Rieman and McIntyre (1995) analyzed bull trout occurrence in relation to large-scale habitat variability in the Boise River basin of Idaho. They found occurrence to be positively related to two measures of habitat size: stream width and patch (stream catchment) area. This suggested that habitat size may play an important role in the persistence of bull trout populations. A second geometrical feature of fragmented habitats, patch isolation, also may be important to population persistence (MacArthur and Wilson 1967, Kindvall and Ahlén 1992, Hanski et al. 1996, Sjögren-Gulve and Ray 1996). Furthermore, the effects of reduced habitat area and increased isolation may act together to increase the risk of extinction of species in fragmented landscapes (Fahrig and Merriam 1994). Here, we combined data from the original 46 habitat patches considered by Rieman and McIntyre (1995) with data from an additional 35 patches surveyed in the Boise River basin in 1993–1994 to look for evidence of such effects. Isolation was defined as stream distance separating a particular patch from the nearest occupied patch in a drainage network. Because drainage networks are linear systems, dispersal can only occur in an up- or downstream direction, a constraint that may increase vulnerability of stream-living organisms to habitat fragmentation (Zwick 1992, Rieman and McIntyre 1995, Nakano et al. 1996, Rahel et al. 1996, Dunham et al. 1997).

Apparent influences of patch isolation may alternatively be due to spatially correlated environmental conditions within a drainage network. Accordingly, spatial proximity of habitats may lead to correlated population dynamics (Harrison and Quinn 1989), and relationships between patch isolation and occurrence may be due to spatial correlation in unmeasured habitat characteristics, rather than to dispersal alone. To distinguish these alternative explanations, we tested for spatial independence of bull trout occurrence (spatial autocorrelation) using straight-line, rather than stream distance between patches, regardless of patch occupancy (occupied or absent). Recent work on other fish has shown that spatial autocorrelation may strongly affect inferences about large-scale distributional patterns (Hinch et al. 1994, but see Rieman and McIntyre 1996).

While Rieman and McIntyre (1995) considered habitat size, and possibly isolation, to play a key role in the persistence of bull trout populations, an analysis of purely geometrical factors may not provide specific information on factors that directly govern rates of extinction and recolonization within habitat patches (Sjögren-Gulve and Ray 1996). Rieman and McIntyre (1995) considered only stream gradient as an alternative to patch size (stream width or patch area) to explain bull trout occurrence. Here, we examined patch-scale patterns of bull trout occurrence in relation to three additional factors, including occurrence of nonnative brook trout *Salvelinus fontinalis*, road density, and solar radiation.

Nonnative brook trout are frequently implicated in the decline of bull trout, impacting populations through introgressive hybridization, and possibly through interactive segregation (reviewed in Rieman and McIntyre 1993). The negative impacts of roads on salmonid habitats are well known, and include increased erosion and sedimentation of stream basins, alterations in stream channel morphology, changes in flow regimes, migration blockage, and increased human access (Furniss et al. 1991, Lee et al. 1997). Aspect and solar radiation may affect stream temperatures and bull trout, which appear to be associated with relatively cold water temperatures (Fraley and Shepard 1989, Rieman and McIntyre 1993, Rich 1996, Buchanan and Gregory 1997, Rieman et al. 1997*b*).

While the central focus of this study was on patch-scale patterns, we also considered relationships at smaller spatial scales. Distributional patterns of species in landscapes may be the product of several processes operating on different spatial and temporal scales (Wu and Loucks 1995). Recent work on other salmonids, for example, has clearly demonstrated the importance of considering multiple scales (cf. Fausch et al. 1994, Dunham and Vinyard 1997, Wiley et al. 1997). Our sampling design emulated previous hierarchical clas-

TABLE 1. List of variables, units of measurement, and spatial scales at which variables were analyzed. See *Methods* for definition of site, stream, and patch terms.

Variable	Units	Scale
Brook and bull trout occurrence	category (0, 1)	site, reach, patch
Stream width	m	reach
Stream gradient	percent	reach
Solar radiation	$\mathrm{GJ \cdot m^{-2} \cdot y^{-1}}$	patch
Road density	m/ha	patch
Patch area	ha	patch
Distance to nearest occupied patch	m	patch

sifications of stream habitats (Frissell et al. 1986), and covered spatial scales ranging from 10 to 10^5 m (Table 1).

In particular, we focused on segregation between brook trout and bull trout, as previous work has emphasized the importance of scale-dependent interactions in other stream-living *Salvelinus* species (Fausch et al. 1994). We also analyzed bull trout occurrence among stream reaches within occupied patches in an attempt to resolve collinearity between stream width and patch size observed by Rieman and McIntyre (1995). We considered the influence of both stream width and gradient on bull trout occurrence among stream reaches within occupied patches.

Our primary aim in this study was to determine the status of bull trout in the Boise River basin with regard to potential factors affecting occurrence. Resulting patterns of bull trout occurrence in relation to physical, biotic, and geometrical factors were then evaluated to determine the relevance of alternative models of metapopulation structure (Harrison and Taylor 1996). In addition, the influences of potentially confounding factors (scale dependence, spatial autocorrelation, multicollinearity) were considered in the analysis. Collectively, these results were used to evaluate the efficacy of presence–absence analyses (incidence functions) as a practical approach to studying metapopulations in complex landscapes, such as those inhabited by bull trout.

METHODS

Study areas were described in detail by Rieman and McIntyre (1995). Study areas were located in the upper Boise River basin in southwestern Idaho, which consists of three major subbasins (North Fork, Middle Fork, and South Fork), covering ~5700 km² (Fig. 1). These three subbasins were all isolated from the lower Boise River by dams constructed prior to the 1950s. Bull trout populations in the South Fork Boise River are presently isolated behind Anderson Ranch Dam, while those in the North and Middle Forks are potentially interconnected.

Bull trout exhibit a variety of life history patterns. Juveniles typically rear in natal or adjacent streams for 2–3 yr. Some fish may assume a "resident" life history, remaining in the natal or closely associated streams for life, while others may migrate to larger rivers or lakes, returning to the natal streams at maturity to spawn (Rie-

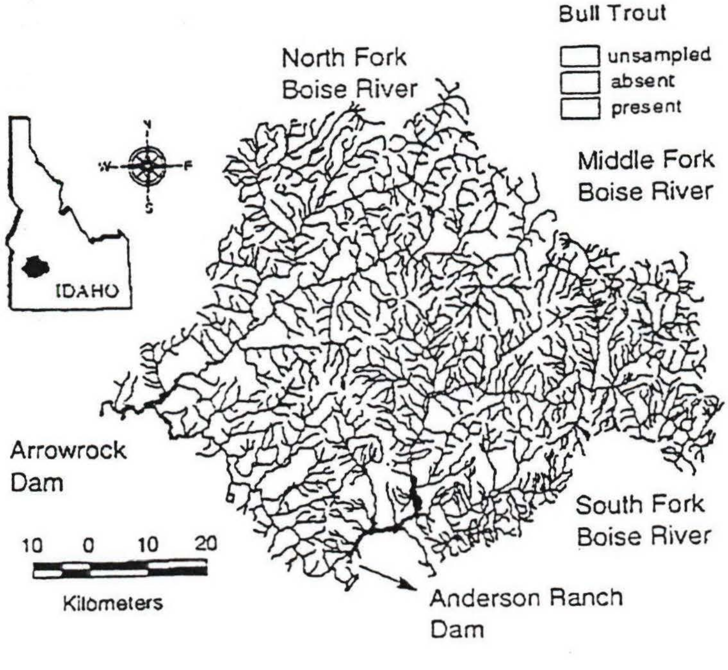

FIG. 1. Map of Boise River basin, west-central Idaho, showing outlines of 104 habitat patches (stream catchments) within the basin. Shading indicates patches occupied (present) or unoccupied (absent) by juvenile bull trout, and unsampled patches.

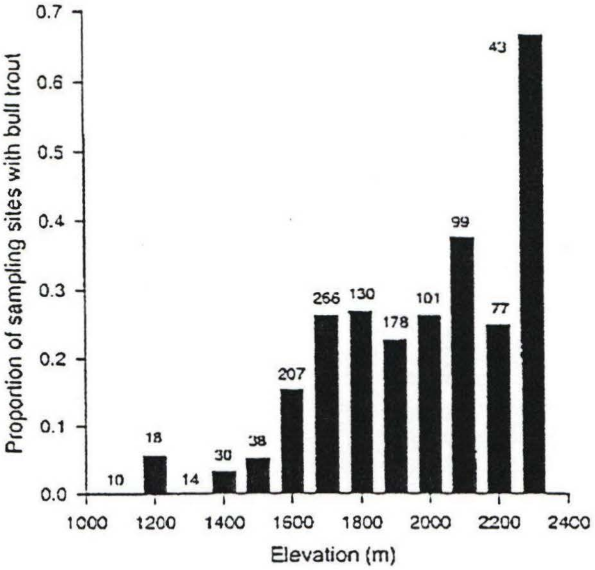

FIG. 2. Occurrence of small (<150 mm) bull trout from 1045 sample sites distributed across a gradient of stream size and elevation in 18 streams including and surrounding the Boise basin that were known to support extant bull trout populations. Numbers over bars indicate number of samples in each bin. Data include those reported in Rieman and McIntyre (1995, their Fig. 2) and additional observations from studies conducted by the U.S. Forest Service Rocky Mountain Research Station, Boise, Idaho, and are independent of the work reported in this paper.

man and McIntyre 1993). Larger, migratory bull trout may occur throughout the Boise River basin and similar systems (Rieman et al. 1997*a*, Swanberg 1997). Our observations of juvenile fish, however, suggest spawning and initial rearing occur almost exclusively in higher elevation headwater streams (Fig. 2; also see Rieman and McIntyre 1993, Swanberg 1997). Bull trout distributions and densities have been consistently linked with colder waters than those of other salmonids (Rieman and McIntyre 1993, Buchanan and Gregory 1997), so this pattern is presumably a result of a temperature constraint or preference (Rieman and McIntyre 1995). Other details of bull trout life history can be found in Pratt (1992), and Rieman and McIntyre (1993).

Habitat selection by salmonid fishes may be reinforced through strong breeding-site fidelity (homing, Dittman and Quinn 1996), and, consequently, local breeding populations of stream-living salmonids are best defined on the basis of the distribution of smaller, presumably "premigratory" or resident individuals (Allendorf and Waples 1995, Rieman and McIntyre 1995). Migratory or large resident bull trout adults may use habitats well outside of areas used for spawning and initial rearing (Pratt 1992, Rieman and McIntyre 1993, Swanberg 1997). These larger fish and the habitats they use may be important in terms of among-patch dispersal and other life history characteristics, but patch structure must be defined according to the condition that constrains the reproductive portion of the life cycle (Haila et al. 1993, Hanski 1996). For bull trout, this is represented by headwater stream networks (Rieman and McIntyre 1995). Recent work with similar bull trout populations has confirmed genetic structuring among tributary populations at this scale (P. Spruell and F. W. Allendorf, University of Montana, *unpublished data*). Based on observed distributions of juvenile bull trout (<150 mm), Rieman and McIntyre (1995) defined habitat patches as the stream catchments above 1600 m elevation and with an accessible perennial stream. Watersheds <400 ha were not included in the analysis because they rarely supported perennial streams large enough to support fish. We retained that definition for this analysis and identified a total of 104 potential habitat patches throughout the basin (Fig. 1).

Sampling of stream habitats and fish occurrence followed methods in Rieman and McIntyre (1995). Fish sampling intensity was evenly distributed among all habitat patches and involved electrofishing or snorkeling (Rieman and McIntyre 1995). To determine occurrence within patches, sampling was conducted in one to three reaches of the main stem of each patch. The term "main stem" refers to the largest perennial stream draining a patch. Each reach was ~0.5 km in length and contained five sample sites, each 30 m in length. Sampling continued until bull trout were detected, or when three reaches, located in the lower, middle, and upper portions of the main stem were sampled, unless the middle or upper portions of the streams clearly had become too small to support fish.

Assuming a minimum detection efficiency of 0.25 for each site, a Poisson sampling distribution, and minimum density of 15 fish/km in a 10-km stream, Rieman and McIntyre (1995) estimated a minimum detection efficiency of 0.82 for cases where all three reaches were sampled. Recent comparisons of day and night snorkeling to electrofishing estimates of bull trout abundance in a nearby stream suggest minimum detection efficiencies were actually much higher (Thurow and Schill 1996). Accordingly, detection efficiencies in this study may be much larger than 0.82, but it is possible that some "false absences" were recorded during surveys (e.g., Reed 1996). We assumed most false absences, if present at all, were likely due to very small population sizes. Such small populations are likely to be at high risk of extinction, and therefore destined to become bona fide absences in the near future (Lande 1993).

To consider factors that may influence bull trout distributions at finer scales, we sampled additional sites and reaches in tributary streams within occupied patches. Reaches in tributaries were at least 500 m above the mouth of the stream, but because of problems with access they were not randomly or systematically distributed across the accessible length of a stream. Sites (30 m) represented the smallest spatial scale (10 m), reaches (0.5 km) represented an intermediate spatial scale (10^2 m), and patches represented the largest spatial scales ($\geq 10^3$ m) for the subsequent analysis. This sampling strategy emulated hierarchical classification of stream habitats (e.g., Frissell et al. 1986), and permitted an analysis of processes occurring at different spatial scales. A total of 81 of 104 potential patches (Fig. 1), 179 reaches, and 720 sites were sampled for occurrence of bull trout.

Fish occurrence, stream width, and gradient were measured following Rieman and McIntyre (1995). Briefly, brook trout and bull trout were considered present in a patch, reach, or site if any individuals were observed in the relevant samples. Wetted widths were taken at a random point for each site and averaged for a reach. Because sampling occurred during late summer, widths approximated base flow conditions. Stream gradients were measured at each site with a clinometer and averaged for a reach. Patches were identified as the catchments above 1600 m and delineated from U.S. Geological Survey 30 m Digital Elevation Models (DEM) using ARC/INFO GRID 1 extension. An estimate of annual solar radiation was assigned to each 30-m grid cell in each patch based on the slope and aspect of the cell and approximated annual solar radiation for 63 slope–aspect classes from Buffo et al. (1972). The estimates for each cell were averaged for the patch. Road densities were calculated as the total length of all forest system roads within a patch divided by patch area. Digitized road coverages were provided by the Boise National Forest, Boise, Idaho.

Interpatch distances were calculated as the minimum distance between patches along the network of streams connecting those patches, using the ARC/INFO NETWORK extension and the U.S. Geological Survey 1:24 000 digitized hydrography. Interpatch distances were calculated only where the connecting stream corridors were not blocked by dams or natural barriers to fish dispersal. We considered distance to nearest occupied patch as a measure of patch isolation (Table 1). Factors other than linear stream distance (e.g., isolation due to other biotic or physical barriers) were not considered in the analysis. Isolation may be indirectly related to environmental factors that could affect migratory behavior, such as proximity to downstream feeding habitats (e.g., large rivers, lakes, reservoirs). Habitats in areas with a greater probability of supporting migratory individuals may be more likely to support bull trout for at least two reasons. First, migratory individuals generally are larger, and therefore may have greater reproductive potential. Second, migratory individuals use areas outside of spawning and rearing habitat, therefore reducing the chance that disturbance to such habitats will extirpate all individuals in a breeding population ("risk-spreading" in space, den Boer 1968). Because little is known in general about life history variability in bull trout and relations to dispersal behavior, we considered only the simplest measure of patch isolation (Table 1). Another issue with our measure of isolation concerns the potential effects of dams in the Boise basin. A major dam prevents bull trout movement between formerly connected habitats in the South Fork Boise River from other habitats in the Boise basin. We did not consider such long-distance dispersal in this study, and the dam had no influence when distance to nearest occupied patch was considered (see Fig. 1).

Data analyses began with patterns of patch-scale bull trout occurrence (Table 1). All data analyses used logistic regression (Hosmer and Lemeshow 1989, SAS Institute 1995). Best subsets logistic regression (SAS Institute 1995) was initially used to screen the five patch-scale predictors (Table 1). Logistic regression analysis, in contrast to other methods (e.g., discriminant function analysis, ordinary least-squares regression), is considerably more flexible in terms of model assumptions, such as the assumption of a linear relationship between response and predictor variables, normality, and equal variance among groups. If, however, these conditions are satisfied, the power of logistic regression to detect relationships may be increased (Tabachnick and Fidell 1996). Log_{10} transformations of patch area, interpatch-patch distances, and solar radiation, and an inverse transformation of road density, resulted in the best fitting model (using the score statistic, Hosmer and Lemeshow 1989, SAS Institute 1995). Unless otherwise specified, all further references to these variables refer to transformed values. Jackknifed classification rates from logistic regression models were calculated using SAS (SAS Institute 1995).

Multicollinearity among predictor variables was first addressed by evaluating pairwise correlations. A second, common multicollinearity diagnostic, the variance inflation factor (VIF), was estimated by regressing each predictor variable in relation to others in the model. Variance inflation factors estimate how much the variances of regression coefficients are inflated relative to the case when predictor variables are not linearly related (orthogonality). The VIF for each variable was calculated as $1/(1 - R^2)$, where R^2 is the coefficient of determination from ordinary least-squares regression of a predictor variable in relation to all other predictors in the model (Phillipi 1994). Variance inflation factors of 10 or greater were considered to indicate problems with multicollinearity (see Phillipi 1994). Finally, we evaluated the possible influence of collinearity by checking the sensitivity of parameter estimates from logistic regressions to removal of each predictor variable (Hosmer and Lemeshow 1989).

Spatial autocorrelation in patch-scale occurrence of bull trout was examined with Mantel tests (Fortin and Gurevitch 1994). The Mantel test is used to test for associations between pairwise distance matrices (Manly 1997). We used Mantel tests to look for associations between pairwise distances between patches and bull trout occurrence. Pairwise distances between patches were estimated from Universal Transverse Mercator

TABLE 2. Results of variable selection with best subsets logistic regression of patch-scale bull trout occurrence.

Number of variables	Score value	Variables included in model
1	14.83	patch area
1	14.17	stream distance to nearest occupied patch
2	28.07	patch area, stream distance to nearest occupied patch
2	23.75	patch area, road density
3	30.95	patch area, stream distance to nearest occupied patch, road density
3	28.70	patch area, stream distance to nearest occupied patch, solar radiation
4	32.24	patch area, stream distance to nearest occupied patch, road density, solar radiation
4	30.95	patch area, stream distance to nearest occupied patch, road density, brook trout
5	32.31	all patch-scale predictors (see Table 1)

(UTM) map projections. Euclidean distances between all pairs of patches were calculated with X–Y coordinates determined as eastings and northings, respectively, measured in meters. Both linear and inverse Euclidean distances were used in Mantel tests of spatial autocorrelation. Values in the pairwise matrix of bull trout occurrences were coded as zeros when both patches shared the same state (e.g., both habitats were either occupied or not occupied), and as ones when they were in different states (e.g., occupied vs. not occupied). This coding was similar to design matrices used by Fortin and Gurevitch (1994).

Mantel tests were conducted with the "R" package for spatial analysis (Legendre and Vaudor 1991). The Mantel Z statistic was normalized (r) so that r values varied between -1 and 1, similar to the familiar values of Pearson's linear correlation coefficient (Fortin and Gurevitch 1994). The significance of r values was evaluated with a reference distribution of r values created by Mantel tests on 9999 randomizations of matrix elements, which also contained the original r value for a total of 10 000 observations (see Jackson and Somers 1989, Manly 1997).

Finally, covariation between bull trout occurrence and selected variables was analyzed at smaller spatial scales with logistic regression. Stream width and gradient were analyzed in relation to variability in bull trout occurrence among stream reaches within occupied patches only. Restricting the analysis of stream width and gradient to reaches within patches was necessary to distinguish width (and potentially gradient) effects due to habitat selection by bull trout, as hypothesized by Rieman and McIntyre (1995). Previous analyses could not distinguish patch-scale stream width and patch-area effects due to collinearity (Rieman and McIntyre 1995).

Because results of the patch-scale analysis strongly suggested that bull trout may not have free access to stream habitats in unoccupied patches, due in part to patch isolation, we restricted the analysis of stream width and gradient effects to variability among stream reaches within occupied patches. Similarly, co-occurrence of bull trout and brook trout was analyzed among stream reaches and sites within patches occupied by bull trout (brook trout effects were not significant at the patch scale, where all potential patches were analyzed). Segregation between potentially interacting species may be more apparent at smaller spatial scales, especially for stream-living salmonids, which typically defend holding positions within streams, while larger scale patterns may result from large-scale variability in abiotic factors (Fausch et al. 1994).

RESULTS

Patch-scale analyses

In all, 81 patches were used in patch-scale analyses of bull trout occurrence. Bull trout were present in 29 patches and absent in 52. Based on the score criterion (Hosmer and Lemeshow 1989), a logistic regression model of bull trout occurrence with four predictors (patch area, distance to nearest occupied patch, road density, and solar radiation) was selected as the best subset (Table 2). Logistic regression analyses of the four-variable model revealed a highly significant and positive relationship between bull trout occurrence and patch area, and inverse relationships with distance to nearest occupied patch and road density (Table 3, Fig. 3). Solar radiation was not significant ($P = 0.16$) and was dropped from the model. Pairwise interactions were tested among all significant predictors and none

TABLE 3. Results of logistic regressions of patch-scale bull trout occurrence (transformed predictors, see *Methods*). Values in parentheses are lower and upper 95% confidence limits for parameters estimates.

Variable	df	Parameter estimate	SE	Wald chi-square	P
Intercept	1	−3.2	3.49	0.84	NS
Patch area	1	1.26 (0.61, 2.05)	0.36	12.05	0.0005
Distance to nearest occupied patch	1	−0.84 (−1.48, −0.30)	0.30	8.10	0.004
Road density†	1	1.59 (0.07, 3.19)	0.79	4.10	0.04

† Note that the sign of the slope parameter estimate for road density is for an inverse transformation, and thus the sign is reversed from that expected with untransformed data.

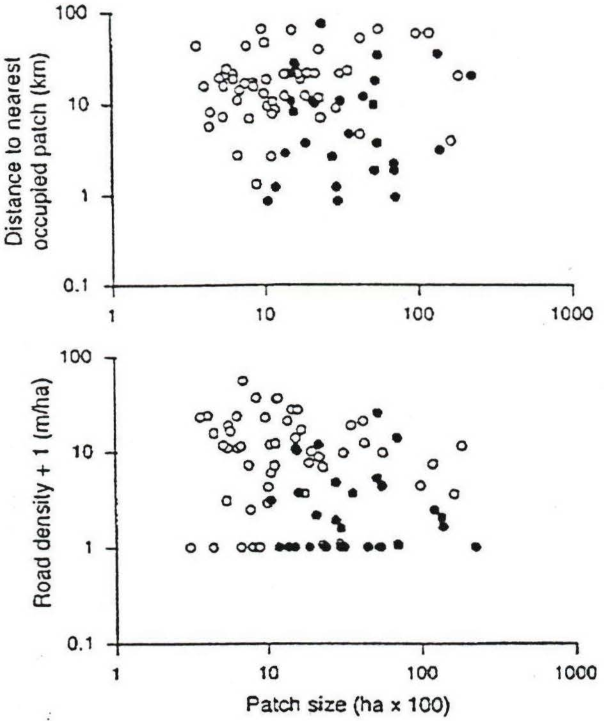

FIG. 3. Relationships between bull trout occurrence (solid circles = present, open circles = absent) and patch size, distance to nearest occupied patch (top), and road density (bottom). An $X + 1$ transformation was necessary to display road density values of zero.

were detected. The resulting model (Table 3) correctly predicted >80% of bull trout occurrences at the 0.50 probability cutoff.

Multicollinearity.—A highly significant correlation between distance to nearest occupied patch and road density was apparent ($r = -0.41$, $P = 0.0002$). The potential influence of this collinearity on variance inflation and regression coefficients was therefore evaluated in more detail. Regressions of the predictor variables in Table 2 (results not shown) indicated that none of corresponding VIF values was >1.25, while the average VIF of all variables was 1.16. This value indicates that multicollinearity is of little concern (Phillipi 1994). Separate logistic regressions of bull trout occurrence with and without road density and distance to nearest occupied patch were conducted to test if the inclusion (or exclusion) of either in the model affected parameter estimates (see Hosmer and Lemeshow 1989). From the results in Table 4, it can be seen that point estimates of regression slopes do change to a small degree. Confidence limits for regression slopes (Table 3) indicate that these changes are of little significance, however.

TABLE 4. Results of logistic regressions of bull trout occurrence to evaluate the potential influence of multicollinearity. See *Results* for details.

Variable	df	Parameter estimate	SE	Wald chi-square	P
a) Model without distance to nearest occupied patch					
Intercept	1	−10.58	2.57	17.00	0.0001
Patch area	1	1.18	0.318	13.67	0.0002
Road density	1	2.27	0.71	10.08	0.0015
b) Model without road density					
Intercept	1	−0.75	3.18	0.06	0.81
Patch area	1	1.27	0.35	13.05	0.0003
Distance to nearest occupied patch	1	−1.04	0.29	12.86	0.0003

TABLE 5. Mantel matrix correlations of bull trout occurrence in relation to two measures of interpatch distance. Probabilities are for a one-tailed test (to test alternative hypothesis that geographically proximate sites are more similar).

Distance	r	P
Euclidean	0.30	0.12
Inverse Euclidean	−0.29	0.15

Spatial autocorrelation.—Mantel tests with Euclidean and inverse Euclidean measures of pairwise geographic distances indicated that bull trout occurrence was not spatially autocorrelated among patches (Table 5). A plot of bull trout occurrence in relation to geographic distances similarly showed no obvious spatial patterns (Fig. 4).

Analyses at finer spatial scales

Logistic regression indicated bull trout occurrence among stream reaches within occupied patches ($n = 72$) was positively related to stream width (Wald $X^2 = 6.09$, $P = 0.01$). Occurrence of bull trout in stream reaches was not related to stream gradient. Logistic regression of bull trout occurrence in relation to oc-

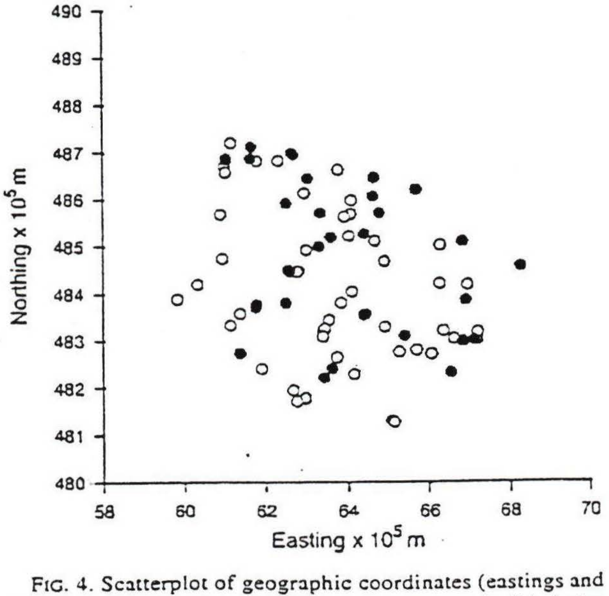

FIG. 4. Scatterplot of geographic coordinates (eastings and northings, in meters), and bull trout occurrence (solid circles = present, open circles = absent) in the Boise River basin.

currence of brook trout revealed no significant associations at patch, stream, or site scales.

DISCUSSION

Results of this study confirm earlier findings (Rieman and McIntyre 1995) that habitat size may play an important role in the patch-scale persistence of stream-living bull trout populations. It also appears that patch-scale persistence may depend on habitat connectivity and human disturbance in the form of road density. Within occupied patches, bull trout were found to select wider stream habitats, but gradient and occurrence of nonnative brook trout did not explain bull trout occurrence.

Factors affecting patch-scale persistence of bull trout

Habitat size may be positively related to local population persistence for at least two reasons. First, larger habitats may support larger populations. Larger populations should be less vulnerable to extinction due to stochastic demographic factors, and may be less vulnerable to the effects of environmental variability and catastrophes (Lande 1993). The effects of environmental variability and catastrophes on population persistence may interact with habitat complexity, which may be greater in larger stream habitats (Frissell et al. 1986, Schlosser 1987). In large habitats, localized disturbances are less likely to affect all segments of a population, thus reducing the chance that all individuals will be killed or displaced by a single event (Harrison and Quinn 1989). Effects of physical disturbance in stream basins may be very localized (Resh et al. 1988, Reeves et al. 1995, Schlosser 1995, Rieman et al. 1997*a*), and thus populations in larger and more complex stream basins may be more resistant to local extinction. It is possible that habitat size may increase population vulnerability, by facilitating occurrence of predators (Sjögren-Gulve 1994), for example, or by intensifying intraspecific competition when resources are concentrated around habitat edges (Pearman 1993). Such does not appear to be the case for bull trout in this study, however.

The significant relationship between distance to nearest occupied patch and bull trout occurrence suggests dispersal also may be important to local population persistence (Fig. 5). The potential for spatial autocorrelation due to unmeasured environmental characteristics was examined but rejected as a likely alternative explanation to dispersal. Some bull trout have been shown to move over relatively long (>50 km) distances in streams (Bjornn and Mallet 1964, Swanberg 1997). Larger (>150 mm) individuals may undergo extensive seasonal feeding and spawning migrations within stream basins (Swanberg 1997), but juveniles and resident individuals may be restricted in their movements (Rieman and McIntyre 1993). Some bull trout may easily move the distances separating local populations in the Boise River basin. We know little, however, about the actual rates of dispersal (or "straying" of reproducing adults from natal habitats) necessary to link those populations demographically. It is reasonable to assume that such dispersal is more likely among populations that are closer together, and that it is more likely in populations with migratory life history patterns than in those that are strictly resident. The relationship between dispersal and migration of small bull trout in relation to life history variability is a critical area of uncertainty (see *Implications for metapopulation structure*).

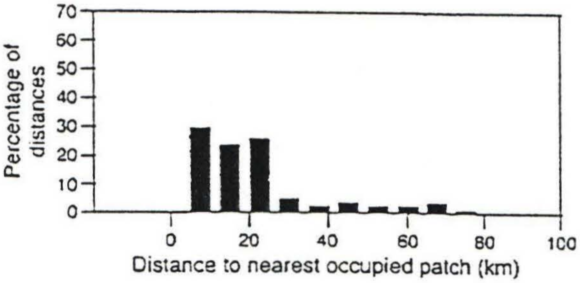

FIG. 5. Distribution of distances to nearest occupied patch for 81 patches of potentially occupied bull trout habitat in the Boise River basin.

We found that bull trout occurrence was negatively related to density of roads within stream basins. Roads increase human access to streams, which may facilitate increased angling mortality and introductions of nonnative salmonids (Furniss et al. 1991, Lee et al. 1997). Erosion and sedimentation caused by roads may lead to stream channel instability and habitat degradation that may increase vulnerability of bull trout as well (Rieman and McIntyre 1993). Details of road location, construction methods, and variability in local geology and hydrologic regimes may all affect the impact of roads on salmonid habitats (Furniss et al. 1991), which may lead to greater variability in the response of bull trout populations. Roads also are related to other human land uses, such as mining, timber harvest, and livestock grazing, which may affect the quality of salmonid habitat (see papers in Meehan 1991). In spite of these potential sources of variability, the significant association of roads with distribution of bull trout in the Boise River basin and across the region (Rieman et al. 1997*b*, Baxter et al. *in press*) suggests that the negative effects of road-related impacts may be pervasive.

Implications for metapopulation structure

Relationships between variability in patch quality (e.g., size, carrying capacity, and productivity), patch spacing, and dispersal are the key elements determining the structure and dynamics of metapopulations (Hanski and Simberloff 1996, Harrison and Taylor 1996, Fig. 6). Patch size (area) was the single most important factor determining bull trout occurrence in this study, and variability in patch area is large (Fig. 7). Patterns

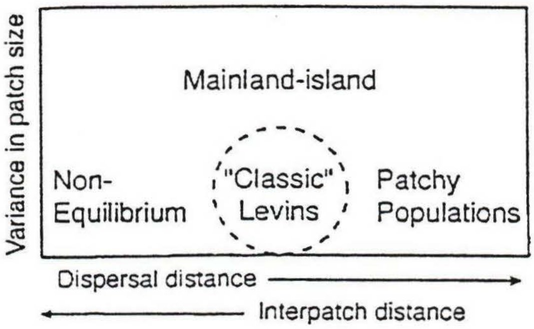

FIG. 6. Metapopulation structure in relation to variance in patch size, dispersal distance, and interpatch distance (modified from Harrison and Taylor 1996). See *Methods* for definition of terms.

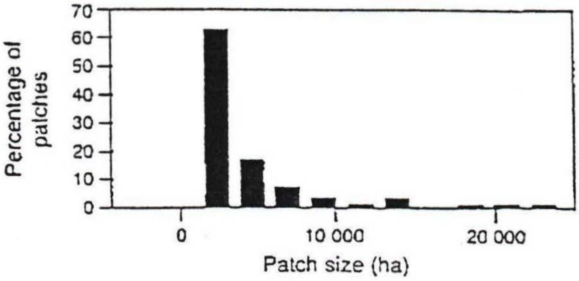

FIG. 7. Distribution of sizes (areas) for 81 patches of potentially occupied bull trout habitat in the Boise River basin.

of occurrence for Boise River bull trout are not consistent with the simple metapopulation structure envisioned by Levins-type models (Harrison and Taylor 1996). Resolution of where bull trout metapopulations in the Boise River basin may lie along other parts of the continuum of potential configurations (Fig. 6) is restricted by lack of direct information on rates of dispersal and local extinction.

If we assume that long-distance dispersal is frequent, and that local extinctions are more likely to occur in smaller habitat patches, then we may reasonably conclude that Boise River bull trout lie somewhere along the continuum between mainland-island and patchy metapopulation configurations (Fig. 6). Alternatively, if dispersal is restricted, Boise River bull trout must lie somewhere between nonequilibrium and mainland-island metapopulation configurations. If Boise River bull trout are in an mainland-island configuration, then some local populations may be relatively persistent (e.g., those in large patches), while others may be more ephemeral, perhaps functioning as population sinks (Pulliam 1988). On the ends of this continuum, bull trout may exist in a nonequilibrium state, where all local populations are destined for extinction due to restricted dispersal (and presumably recolonization), or as a patchy metapopulation, where high rates of recolonization lead to high rates of patch occupancy (Harrison and Taylor 1996, Fig. 6). Several lines of evidence suggest bull trout in the Boise River basin may consist of a complex metapopulation structure that is a composite of these possibilities.

Overall, we found bull trout in 36% of potentially occupied habitat patches in the Boise River basin. If dispersal was widespread and local extinctions were relatively uncommon throughout the basin, we should have observed much higher occupancy rates. At finer spatial scales, Rieman et al. (1997*a*) observed rapid (<3 yr) recolonization of defaunated bull trout habitats following severe fires in tributaries of the Boise River. Rapid recolonization was likely facilitated both through complex life-histories with overlapping generations, and through movements within local stream systems. These observations suggest that the complexity of habitats played a key role in the persistence of bull trout populations influenced by the fires (Rieman et al. 1997*a*). Because the complexity and diversity of stream habitats are expected to vary directly with patch (catchment) size (Frissell et al. 1986, Schlosser 1987, Rieman and McIntyre 1995), the risk of local extinction should as well. The few large ($>10^5$ ha) occupied patches may possibly serve as important sources of bull trout for recolonization of unoccupied habitat within the Boise River basin, and parts of the basin may function as mainland-island or patchy metapopulations (Fig. 6).

Bull trout populations in the Pacific Northwest are generally believed to be in a state of decline (Rieman and Myers 1997, Rieman et al. 1997*b*). Although there is no clear evidence of such a trend in the Boise River basin, fishing and habitat disruption have occurred at potentially important levels across the system. The association of bull trout occurrence with road density is an indication of such effects. If populations are in a general state of decline across the basin, the significant patch-area effect could emerge simply as an artifact of smaller populations disappearing more quickly. We suggest it is unlikely that these bull trout populations are strictly in a nonequilibrium decline, because distance to nearest occupied patch was also a significant predictor. This suggests that some recolonization does occur at broader scales. A number of patches are also found within Forest Service Wilderness or roadless areas with very limited access, and the area effect is still apparent (e.g., patches with low densities of roads in Fig. 3). Populations in these areas have likely been influenced little by habitat disruption or fishing.

Dispersal behaviors are complex, and may be a function of several biotic and abiotic processes operating on different spatial and temporal scales (Ims 1995, Ims and Yoccoz 1996). Habitat fragmentation itself may directly affect dispersal behaviors of animals (Ims 1995, Yahner and Mahan 1997). Fragmentation of stream habitats may have effects that parallel restricted dispersal observed for salmonid populations that are isolated above waterfalls (Jonsson 1983, Northcote and Hartman 1988, Northcote 1992). In such cases, the potential benefits of movement (Northcote 1992, Jonsson

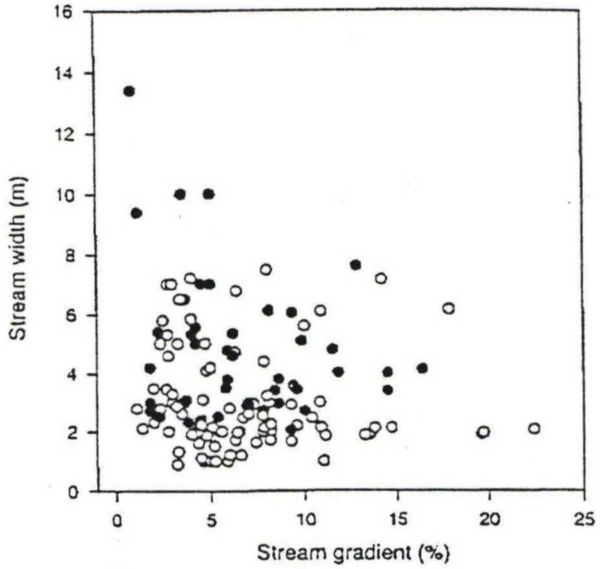

FIG. 8. Relationships between bull trout occurrence in stream reaches within occupied patches and stream width and gradient (solid circles = present, open circles = absent).

and Jonsson 1993) are clearly outweighed by costs. Bull trout, like many salmonids, may consist of several life-history "forms" with different dispersal or migratory behaviors (Rieman and McIntyre 1993, Willson 1997). Relationships between bull trout life histories, habitat structure, and the potential for habitat fragmentation to restrict dispersal of bull trout clearly require further research.

Patterns at smaller spatial scales

Rieman and McIntyre (1995) found patch-scale occurrence of bull trout in the Boise River basin to be positively related to both patch area and stream width, but not to stream gradient. Because patch area and stream width were correlated, they could not distinguish the effects, and hypothesized that width effects may be due to habitat selection by bull trout. The positive relationship between bull trout occurrence and stream width within occupied patches found in this study supports their explanation. A pattern similar to patch-scale relationships (Rieman and McIntyre 1995) emerged within patches (Fig. 8). Bull trout were found only in streams >2 m in width, even with free access to many smaller habitats within occupied patches (see also Figs. 2 and 3 in Rieman and McIntyre 1995). There are several instances in which bull trout were not found in streams >2 m in width, and this may be due to low densities of fish, perhaps resulting from past disturbances (Platts and Nelson 1988), or to avoidance of some other feature of the habitat.

Analyses of co-occurrence of bull trout and brook trout at stream and site scales revealed no associations, suggesting bull trout and brook trout do not segregate among habitats at spatial scales considered in this study. We strongly caution that the possibility of competition between bull trout and brook trout cannot be ruled out by this result, because co-occurrence data may be misleading (Hastings 1987). Segregation may occur at smaller spatial scales (e.g., among microhabitats within sites), especially if feeding territories are defended (Grant and Kramer 1990, Fausch et al. 1994, Nakano and Kaeriyama 1995), but we have no data to evaluate this possibility. Larger scale patterns may emerge through time if bull trout are systematically displaced or replaced by brook trout, or if the reverse were to occur. Interspecific hybridization of bull trout and brook trout could play an important role in replacement of the former by the latter, for example (Leary et al. 1993). Finally, it is possible that the influence of brook trout on bull trout may extend outside occupied patches considered here if the presence of brook trout in downstream areas hinders dispersal through, or occupancy of, downstream habitats (see Fraser et al. 1995).

Conclusions and conservation implications

It has long been recognized that aquatic habitats are organized by processes that can be ultimately traced to landscape-scale influences on stream catchments or watersheds (e.g., Hynes 1975, Frissell et al. 1986). Technological advances in methods to acquire and analyze information on large-scale patterns and processes have dramatically increased the ability of aquatic ecologists to study such phenomena, while at the same time management policies are being revamped to incorporate large-scale perspectives of aquatic ecosystems (Johnson and Gage 1997).

Past analyses, while providing exciting insights on a number of large-scale factors, have often neglected the spatial extent and distribution of landscape elements within stream catchments (Johnson and Gage 1997). For example, assessments of fish–habitat relationships (Hinch et al. 1991) were dramatically modified after spatial autocorrelation of sites was considered (Hinch et al. 1994). In the case of bull trout, metapopulation structure implies suitable habitats are often not occupied, and attempts to relate occurrence of bull trout to habitat characteristics without accounting for patch occupancy are potentially misleading (e.g., Watson and Hillman 1997). As we have shown here for bull trout, the large-scale geometry of stream catchments can strongly influence the distribution of aquatic species, independent of other more commonly considered habitat characteristics. Our analyses revealed that additional factors operating on smaller spatial scales may be important as well. Small-scale factors should be considered together with large-scale patterns, because their effects may otherwise go undetected.

While our study of bull trout was extensive in terms of spatial dimensions, we have limited information to evaluate rigorously the influence of temporal variability. Aquatic landscapes are highly dynamic systems, and long-term data are needed to define more clearly interactions between temporal and spatial processes occurring on different scales (Schlosser 1995, Wiley et al. 1997). Furthermore, we stress the need for better information on parameters related to dispersal success, which can dramatically affect interpretations of spatially explicit population models (including metapopulation models), as recently emphasized by Ruckelshaus et al. (1997).

Our analysis suggests that the actual structure of bull trout metapopulations is highly complex. Real metapopulations of aquatic organisms may be complex mosaics that contain several elements of the structures found in simple conceptual models (Schlosser and Angermeier 1995, Harrison and Taylor 1996). In the case of bull trout and other stream-living fish, habitat spatial structure and life history variability likely function interactively to affect patterns of migration, dispersal, and patch occupancy (Rieman and McIntyre 1993, Gresswell et al. 1994, Schlosser 1995, Schlosser and Angermeier 1995, Willson 1997). These complexities pose important challenges to empirical and theoretical attempts to understand metapopulation dynamics of fish and other aquatic organisms, but insights provided by such studies may prove critical to developing effective long-term management strategies for aquatic ecosystems.

Results of this work have several important implications for management of bull trout. Bull trout populations in larger, less isolated, and less disturbed habitats may be more likely to persist, and these habitats may prove critical in terms of providing long-term refugia and recolonization potential. Disturbance to these populations and their habitats should be minimized. In particular, disturbances associated either directly or indirectly with roads are a critical concern. On the other end of the continuum, small, isolated, and disturbed habitats may be at risk. Management to ensure persistence of these populations may be challenging. In the middle are populations and habitats of intermediate size and/or isolation, where opportunities for conservation and restoration may be greater. Furthermore, the existence of metapopulation structure implies availability of suitable, but presently unoccupied, habitat, which should be managed carefully to facilitate potential natural recolonization or reintroductions of bull trout.

We do not recommend that management activities be prioritized on the basis of this study alone. Clearly, genetic concerns and occurrence of other species of concern merit consideration (see papers in Nielsen 1995). In particular, information on the genetic structure of bull trout populations in the Boise basin would prove useful in terms of prioritizing efforts to maintain genetic diversity. Previous work on bull trout (Leary et al. 1993) and more recent genetic evidence in other basins (P. Spruell and F. W. Allendorf, University of Montana, *unpublished data*) suggest strong genetic divergence among populations, but relatively little within-population variability. One hypothesis to explain this pattern is that current metapopulation structure of bull trout is the result of long-term fragmentation of habitat related to historical changes in regional climate. If so, this implies that dispersal occurs very infrequently and over long periods, perhaps on the order of centuries, and that contemporary losses of local bull trout populations may not be balanced in the near term by recolonization. This time scale may be considerably longer than that hypothesized for dispersal and recolonization for other salmonids (Reeves et al. 1995). We emphasize that further study is needed to define more clearly the temporal scale over which metapopulation dynamics of bull trout occur.

With regard to patterns we observed at smaller spatial scales, it is clear that bull trout select larger habitats, when they are available. However, we caution that results of this study regarding effects of brook trout not be extrapolated to other areas. In other cases within the range of bull trout, negative effects of brook trout on bull trout populations are evident (e.g., Howell and Buchanan 1992, Leary et al. 1993, Rich 1996) and likely scale-dependent, as emphasized above.

A final important issue for managers regards the effects of downstream dams on bull trout in the Boise basin. From a metapopulation perspective, long-term isolation of the South Fork Boise River by dams may restrict long-distance dispersal, the significance of which is unclear at this point. Reservoirs created by downstream dams do support migratory populations of bull trout, and they may be of significance to some local populations (e.g., Rieman et al. 1997*a*). Perhaps most importantly, dams in the Boise basin and further downstream in the Snake River have extirpated runs of anadromous salmon (primarily *Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). The importance of these species to the productivity of aquatic and terrestrial ecosystems (Willson and Halupka 1995) may have affected viability and productivity of bull trout populations directly through loss of a prey base of juvenile salmonids and indirectly through effects on associated species.

ACKNOWLEDGMENTS

We thank D. Myers and M. Radko for their instrumental help with data collection, maps, and GIS support. Many people, but notably, B. Hart, C. Rabe, C. Alexander, L. Leatherbury, T. Busby, and I. Draper, helped with the field work. The Sawtooth and Boise National Forests, and B. Van Skyke, T. Burton, and D. Corely helped with logistical issues and sampling. J. B. Dunham was supported by a Research Joint-Venture Agreement between the University of Nevada–Reno and U.S.D.A. Forest Service Rocky Mountain (formerly Intermountain) Research Station (INT-96089-RJVA), with additional support provided by the Biological Resources Research Center, University of Nevada–Reno. J. Peterson, C. Frissell, C. Ray, and one anonymous reviewer provided excellent and constructive comments on earlier versions of this paper. Thanks to Allann Brothers Co. for providing a stimulating working environment.

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Left Running Head: DISTRIBUTION OF A THREATENED TROUT

Right Running Head: DUNHAM ET AL.

Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout

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Keywords: Lahontan cutthroat trout; Oncorhynchus clarki henshawi; fish distribution; thermal habitat; nonnative fishes; fish habitat.

Abstract.-We investigated local and geographic variability in the up- and downstream distribution limits of threatened Lahontan cutthroat trout (Oncorhynchus clarki henshawi) in stream habitats of the eastern Lahontan basin in northern Nevada and southeast Oregon. At a geographic scale, elevations of upstream distribution limits were significantly correlated with latitude and longitude, suggesting a potential influence of climatic gradients. Elevations of upstream distribution limits also were positively correlated with maximum basin elevation, which suggested topographic, rather than climatic constraints may be important. Upstream distribution limits were not significantly affected by local variation in stream size or presumptive dispersal barriers. Stream gradient was related to upstream distribution limits, but this was again confounded by maximum basin elevation. Stream gradients used by Lahontan cutthroat trout at upstream limits were considerably steeper than those observed for other subspecies of cutthroat trout in other areas. Geographic variation in elevations of downstream distribution limits was also apparent, paralleling variability in summer air temperatures and presumed restriction of Lahontan cutthroat trout from lower elevation habitats by unsuitably warm temperatures in summer. Previous regional models assumed downstream distribution limits for salmonids correspond to isotherms of 22-24°C (mean July air temperature), but we found the distribution of Lahontan cutthroat trout to be considerably more restricted, most closely corresponding to a mean July air temperature of 18°C. Occurrence of nonnative brook trout Salvelinus fontinalis was associated with a significant upstream shift of the downstream distribution of Lahontan cutthroat trout, suggesting a highly variable, but negative interaction between these species.

Lahontan cutthroat trout (Oncorhynchus clarki henshawi) is a threatened subspecies (Office of the Federal Register 40:29864) endemic to the Lahontan basin of northeast California, southeast Oregon and northern Nevada (Coffin and Cowan 1995; Fig. 1). It is estimated that Lahontan cutthroat trout occupies less than 3% of historical habitat in the Walker, Carson and Truckee River basins of northeastern California and western Nevada, and about 14-15% of historical habitat in the eastern Lahontan basin, which includes the Quinn and Humboldt river and Coyote Lake basins (Coffin and Cowan 1995). Like other subspecies of cutthroat trout (e.g. Gresswell 1988; Young 1995; Duff 1996; Hall et al. 1997), the presently contracted distribution of Lahontan cutthroat trout has been attributed primarily to interactions with hatchery and nonnative salmonids, and habitat degradation (Coffin and Cowan 1995).

Most remaining populations of Lahontan cutthroat trout in the eastern Lahontan basin occupy higher elevation, low order headwater stream habitats. The distribution of Lahontan cutthroat trout in these habitats is highly fragmented, and as a result, many populations may be at risk of extinction (Dunham et al. 1997). While it is clear that fragmentation poses a significant threat, factors affecting the distribution of Lahontan cutthroat trout in streams have been quantitatively analyzed only within a limited portion of the basin (Nelson et al. 1992).

Previous work on Lahontan cutthroat trout attempted to explain trout distributions in terms of geologic and geomorphic landscape characteristics (Nelson et al. 1992). Nelson et al. (1992) found trout (both Lahontan cutthroat trout and nonnative brook trout Salvelinus fontinalis) occurred primarily in sites within sedimentary land type associations and hypothesized a connection between land type associations and habitat characteristics that may be limiting trout distributions. While geology and geomorphology may play a potentially important role, several aspects of the study by Nelson et al. (1992) warrant concern. Most importantly, Nelson et al. (1992) suggested that "neither temperature nor dissolved oxygen currently limit cutthroat trout distributions." This statement was based on limited evidence from point samples of water temperature and dissolved oxygen, and anecdotal reports and evidence suggesting Lahontan cutthroat trout may tolerate higher temperatures than other closely related salmonids. A more fundamental issue is that temperature, elevation, and land type associations defined by Nelson et al. (1992) are inextricably interrelated, and therefore temperature cannot be rejected as an important factor.

Several lines of evidence available since the work of Nelson et al. (1992) suggest temperature may indeed be an important factor affecting the distribution of Lahontan cutthroat trout. In the laboratory, Dickerson and Vinyard (in press) found that juvenile Lahontan cutthroat trout can survive short-term (1 h) exposure to water temperatures of up to 26°C, and weekly exposure to constant temperatures of up to 24°C. Patterns of growth and survival suggested an upper chronic exposure limit of 24-25°C, which is not substantially different from information available on closely related salmonids (Dickerson and Vinyard, in press). Our field observations (e.g. Fig. 2) also strongly suggest the distribution of Lahontan cutthroat trout in streams is restricted by unsuitably warm summer water temperatures. Finally, we believe temperature deserves further consideration as an important limiting factor because it has a clear mechanistic (physiological) basis relating it to fitness and habitat quality for salmonids (e.g. Van Winkle et al. 1997).

Another obvious factor potentially affecting the distribution of Lahontan cutthroat trout in streams is occurrence of nonnative trout. Nonnative trout are widespread throughout the range of Lahontan cutthroat trout (Coffin and Cowan 1995). Previous work on geographic variation in salmonid distributions in the region (Keleher and Rahel 1996) considered a coldwater guild consisting of rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), brook trout, and cutthroat trout (*O. clarki ssp.*), without considering potential interactions within this guild. Similarly, previous work on Lahontan cutthroat trout and brook trout in streams (Nelson et al. 1992) did not quantitatively analyze potential interactions between these two species.

In this study, we analyzed downstream distribution limits of Lahontan cutthroat trout in relation to geographic variability and local factors, including occurrence of nonnative salmonids and downstream barriers (e.g. water diversions or natural dewatering). Geographic variability of Lahontan cutthroat trout distributions also was related to thermal distribution limits for trout proposed by Keleher and Rahel (1996) for the region using information on air temperature. Classification of geologic or geomorphic landscape characteristics (Nelson et al. 1992) within the vast study area (Fig. 1) was beyond the scope of this work. As mentioned above, however, it is likely these landscape characteristics and thermal gradients covary with elevation. We did not therefore attempt to distinguish these “alternatives” in this work. Rather, we were interested in the evidence to support the hypothesis that temperature and nonnative salmonids are important factors limiting the distribution of Lahontan cutthroat trout in streams.

We also considered upstream distribution limits of Lahontan cutthroat trout and evidence for geographic variability. Geographic variation in climate (e.g. Mitchell 1976;

Keleher and Rahel 1996) may affect upstream distributions, which may be limited by freezing temperatures in winter (e.g. Cunjak 1996), or reduced growth and survival with colder temperatures and shorter growing seasons at higher latitudes and elevations (Scarnecchia and Bergerson 1987; Shuter and Post 1990; but see Conover 1990). Effects of local factors, including dispersal barriers, channel geometry, and stream gradient were analyzed as well. Dispersal barriers in the form of high stream gradients, steep cascades, or waterfalls (Kruse et al. 1997) may restrict the upstream distribution of cutthroat trout. Stream size may affect trout distributions if fish prefer larger or more complex stream habitats (Kruse et al. 1997; Dunham and Rieman, in press). Stream size also may be related to water temperature (Stefan and Preud'homme 1993).

Methods

Study area and organisms

Lahontan cutthroat trout is endemic to the Lahontan basin of northeast California, southeast Oregon, and northern Nevada (Fig. 1), where it was the only trout species present until translocations of nonnative salmonids began in the late 19th century (Miller and Alcorn 1943; LaRivers 1962). In the last 150 years, Lahontan cutthroat trout has been virtually eliminated from its historical distribution within the western Lahontan Basin, which includes the Truckee, Carson, and Walker River basins, including Lake Tahoe, and Pyramid and Walker Lakes (Coffin and Cowan 1995).

Our study focused on stream habitats in the eastern Lahontan basin, including the Quinn and Humboldt River basins of Nevada, and the Coyote Lake basin of southeast

Oregon (Fig. 1). Here, Lahontan cutthroat trout populations persist as isolated enclaves in low order stream habitats, with the exception of a few basins where favorable conditions in larger downstream habitats may provide demographic connectivity among tributary populations (Coffin and Cowan 1995; Dunham 1996; Dunham et al. 1997).

Descriptions of stream habitats in the eastern Lahontan basin can be found in Nelson et al. (1987), Platts and Nelson (1988), Nelson et al. (1992), Dunham (1996), and Jones et al. (1998). Generally, stream habitats are highly variable in space and time. Within years, however, seasonal fluctuations in stream discharge are fairly predictable. With the exception of episodic flooding from summer thunderstorms, peak discharges generally coincide with spring snow melt and runoff in March-June. Among years, periodic drought conditions contrast with cooler, wetter periods to cause dramatic changes in stream habitats with regard to the frequency and magnitude of stream discharges, water temperature, and physical characteristics of stream channels.

Spatial variation in habitat conditions is also very pronounced. Higher elevation streams are cooler in the summer (<20°C), often with abundant riparian vegetation, pool-forming rocks, and (sometimes) large wood in the channel. Lower elevation streams typically flow through permeable alluvial deposits (Nelson et al. 1992), with degraded (downcut) channels and higher maximum summer water temperatures (>20°C). Stream flows in many lower elevation habitats may become intermittent during summer droughts (Dunham 1996). In winter, colder water temperatures and anchor ice formation may possibly cause high fish mortality in some years.

Stream habitats in the Lahontan basin support a variety of native and nonnative fishes (LaRivers 1962). Nonnative fishes encountered in this study included rainbow trout, brown trout, and brook trout. Brook trout were by far the most common nonnative salmonid present. In the presence of other salmonids, brook trout occurred upstream of other species, with the exception of Lahontan cutthroat trout. Native non-salmonid fishes most frequently encountered included Paiute sculpin (Cottus beldingi), speckled dace (Rhinichthys osculus), mountain sucker (Catostomus platyrhynchus), Tahoe sucker (C. tahoensis), and Lahontan redside shiner (Richardsonius egregius).

The primary land use in the eastern Lahontan basin is livestock grazing (Coffin and Cowan 1995), with localized mining and irrigated agriculture. Recreational fishing for Lahontan cutthroat trout is allowed in Nevada, but is not considered to occur at high enough levels to have significant effects on Lahontan cutthroat trout populations (Coffin and Cowan 1995). We rarely observed anglers on streams in five summers of field work conducted prior to and during this study.

Sampling of distribution limits

Sampling of Lahontan cutthroat trout distributions was conducted from 18 July 1997 to 24 September 1997 during summer base flow conditions. We assumed annual air and water temperatures were at a maximum sometime during this time period. Sampling was initiated in the southern portion of the eastern Lahontan basin and proceeded northward, though time of sampling and distance north were not strongly correlated ($r = 0.42$ $P = 0.03$). We initiated sampling in the south because in 1997 streams there approached summer base flows earlier in the summer. We expected Lahontan cutthroat trout to be well distributed throughout suitable stream habitats in 1997 because the region had experienced three relatively wet and cool years following drought conditions in 1994, and density of fish in many streams in the area has generally increased since 1993 (Dunham 1996, and unpublished data). No attempt was made to collect a random sample of occupied habitats, but samples were interspersed throughout the geographic range of Lahontan cutthroat trout in the eastern Lahontan basin (Fig. 1). A relatively large number of streams was sampled, however (Fig. 1), and we believe our sampling was representative of the range of the subspecies in the eastern Lahontan basin.

Additional data on downstream distribution limits of Lahontan cutthroat trout were obtained from stream survey reports on file at the Nevada Division of Wildlife and Oregon Department of Fish and Wildlife. These data were from a variety of different years and served as a baseline to evaluate results of surveys conducted in 1997. We also used data on upstream distribution limits for three streams surveyed by the Nevada Division of Wildlife in 1997 (J. Elliott, Nevada Division of Wildlife, personal communication). Some populations sampled originated via translocations, either within or outside of the Lahontan basin. Translocated populations included eight of 44 streams sampled for lower distribution limits and five of 45 streams sampled for upstream distribution limits. Translocated populations were carefully scrutinized for their potential influence on the outcome of statistical analyses of the data.

Field sampling of Lahontan cutthroat trout distributions involved locating fish by electrofishing, and then proceeding in an upstream or downstream direction until no fish were encountered for 300 m. Sampling generally proceeded in an upstream direction to maximize the probability of detecting fish. Electrofishing small streams in this manner is an highly efficient method of fish capture. In other work on Lahontan cutthroat trout, capture probabilities from three-pass removal electrofishing (estimated by the program CAPTURE; White et al. 1982) averaged 0.78±0.14 across 138 sites sampled in 1993-5 (JBD, unpublished data). In the final 300 m of sampling, at least 15 relatively high quality pool habitats were fished. High quality pool habitats were defined as those with exceptional cover (e.g. boulders, large wood, undercut banks), and/or deep water.

Initially, distribution limits were determined separately for small (≤100 mm, standard length) and large (>100 mm) fish. Length-frequency distributions for Lahontan cutthroat trout from low and high elevation habitats (Dunham 1996) and age-length relationships from otoliths (JBD, unpublished data) indicate fish less than 100 mm in length may be reasonably classified as juveniles in their first to second year of life (age 0-1 year). This stratification was employed to distinguish the distribution of spawning and early rearing habitat from that used exclusively by larger subadult and adult fish. In all cases, however, the distributions of these two size classes overlapped almost completely, so stratification was unnecessary.

Wetted widths and depths of streams at upstream distribution limits were sampled over a 100-meter reach consisting of 10 transects oriented perpendicular to the wetted stream channel and spaced 10 meters apart, following recommendations in Myers (1995). Average depth at each transect was calculated from depth measurements taken at 25, 50, and 75% of the channel beginning from one bank (depth=0) (Overton et al. 1997). In a few cases, we encountered lack of surface flow or hazardous sampling conditions and less than 10 transects (5-9) were sampled. Maximum depths of all pools, defined according to Hawkins et al. (1993), also were recorded in the 100-meter reach. Stream gradient was estimated directly from 1:24,000 scale topographical maps.

Potential natural and human-caused barriers were noted at distribution limits. Natural physical dispersal barriers consisted of high gradient cascades, waterfalls, and lack of surface flows. Human-caused dispersal barriers included downstream water diversions, and high (>1.5 m, Kruse et al. 1997) vertical headcuts. Presence of non-native salmonids was also documented in each stream. Elevations of upstream and downstream distribution limits were estimated with 1:24,000 scale topographical maps.

Analysis of factors affecting distribution limits

Downstream distribution limits. We initially used ordinary least squares (OLS) regression to develop a predictive model of the elevation of downstream distribution limits of Lahontan cutthroat trout. We considered three predictors, latitude, longitude, and occurrence of nonnative brook trout. Latitude and longitude were estimated by Universal Transverse Mercator (UTM) map projections as northings and eastings, respectively, measured in meters.

Best-subsets regression was used to select variables to be used in regressions. We used a variety of model selection criteria, including summed PRESS residuals, mean square error, Mallows' C_p, Akiake's information criterion, and coefficient of determination for selection of alternative regression models (Freund and Littell 1991). While these diagnostics measure somewhat different dimensions of the data (see Freund and Littell 1991), they generally agree in practice. Variables screened for regressions included linear and quadratic latitude and longitude effects and interaction terms.

Initially, we used data collected during our surveys in 1997 for regression analyses. Other data made available through consultation with state agency biologists were added in subsequent analyses. We initially restricted the analysis to data collected in our own surveys because: 1) many agency surveys were conducted in different years, potentially adding unexplained temporal as well as spatial variability; 2) agency surveys used different survey protocols; and 3) agency survey data were clustered geographically and produced a heteroscedastic distribution of errors (see **Results**).

Distributions of residuals were analyzed to ensure OLS model assumptions of normality and homogeneity of variances were satisfied. Tests for normality used studentized residuals and the W statistic, following the method of Shapiro and Wilk (1965), as implemented by the SAS UNIVARIATE procedure (Cody and Smith 1991). Homogeneity of variances was assessed by correlation of absolute values of studentized residuals with predicted values of the response variable.

When variances were not homogeneous, we compared results of OLS regressions to those generated by percentile regression based on median, rather than mean values of the response (Terrell et al. 1996). Because median values are less affected by outliers and heteroscedastic errors, percentile regression may provide more robust estimates of parameters. We refer to this method as LAD regression, which uses least absolute deviations, rather than squared deviations, as with OLS regression (see Terrell et al. 1996). Confidence intervals for percentile regression estimates were generated by bootstrapping (StataCorp 1997).

The influence of individual observations on regression models was estimated by DFFITS (Myers 1990; Freund and Littell 1991). This diagnostic estimates the number of standard errors the fitted value changes if the $\underline{i}^{th}$ observation is removed (Myers 1990; Freund and Littell 1991). We used a cutoff value of DFFITS = $2(\underline{m}/\underline{n})^{0.5}$, recommended by Belsley et al. (1980), where $\underline{m}$ is the number of parameters (intercept and slopes) and $\underline{n}$ is the number of observations, to judge whether or not observations qualified as influential. Particular attention was paid to streams with downstream diversions or dewatering, as downstream distributions may be truncated in such cases, possibly biasing the regression model.

Since the regression models were intended to be used for predictive purposes, we wished to have a measure of how well our models predicted new observations. Typically model "validation" has involved reserving a subset of observations to be predicted by the original model constructed without these observations. In view of the limited number of data points in our samples, we opted for an alternative that more efficiently utilizes available information. To evaluate the predictive performance of regressions, we used Prediction Sum of Squares (PRESS) residuals (Myers 1990). PRESS residuals were estimated by withholding a single observation ($\underline{y}_i$), and estimating a "residual" by subtracting the observed value from that predicted by a regression model constructed with the remaining ($\underline{n}$-1) observations. This avoids using the observation $\underline{y}_i$ to simultaneously create and evaluate the predictive performance of the regression model.

Upstream distribution limits. The elevation of upstream distribution limits was analyzed as above with OLS regression. Regional variability in upstream distribution limits was modeled as a function of latitude and longitude using UTM coordinates. Local factors, including stream gradient, stream width, average depth, and maximum pool depth, were included in the analysis. Analysis of covariance was initially used to test for the effects of presumptive dispersal barriers on upstream distribution limits. Screening for influential data points was conducted as above using the OLS regression model developed from the full data set. In screening for influential data points, we made special note of streams with potential barriers to upstream dispersal. Dispersal barriers may possibly exclude fish from suitable upstream habitats and distort relationships between upstream distribution limits and other variables.

Because maximum elevations of mountain ranges in our study area follow geographic clines (Grayson 1994), we also tested for geographic variation in the maximum elevation of catchment basins for streams in this study. In other words, it may not be physically possible for Lahontan cutthroat trout to occupy higher elevation habitats in the northern portion of their range because such habitats do not exist. This possibility was considered by analysis of correlations between maximum basin elevation and variables explaining upstream distribution limits of Lahontan cutthroat trout (UTM eastings, northings, and stream gradient, see **Results**).

Correspondence of downstream distribution limits to thermal gradients. Because data on stream temperatures were unavailable, we used mean July air temperature as a surrogate measure, after Keleher and Rahel (1996) and Rahel et al. (1996). We compared our observed downstream distribution limits of Lahontan cutthroat trout to predictions corresponding to the Keleher and Rahel (1996) temperature model:

$$\text{JulyC} = -11.468 + 2.812(\text{latitude}) - 0.007(\text{elevation}) - 0.043(\text{latitude})^2.$$

This model was developed from an extensive air temperature database (n = 615 stations) that included stations from Nevada, as well as the states of Idaho, Montana, Wyoming, Utah, Colorado, Arizona, and New Mexico. This equation was rearranged to predict elevation (meters) from mean July air temperature (JulyC, °C) and latitude (decimal degrees). Latitudes corresponded to coordinates from our observed downstream distribution limits, and predicted elevations of downstream distribution limits were generated with nine temperature models corresponding to mean July air temperatures of 16-24°C. The sum of squared deviations between predicted and observed elevations corresponding to each model was calculated to assess fit (Hilborn and Mangel 1997). The temperature model with the smallest sum of squared deviations was selected as that most closely approximating the air temperature corresponding to the downstream distribution limit of Lahontan cutthroat trout.

Results

Downstream distribution limits

Regression models of downstream distribution limits for streams with and without brook trout were analyzed separately because Levene's test on absolute residuals from analysis of covariance (Kuehl 1994) indicated variability of limits were strongly affected by the presence of brook trout, even when an outlier data point from a stream with a translocated population of Lahontan cutthroat trout was omitted from the data set (F = 5.72, P = 0.02, df = 43). This effect (unequal variances) violated standard ANOVA and regression assumptions (Kuehl 1994), thus invalidating parametric hypothesis tests on all streams combined.

Streams with Lahontan cutthroat trout only. We recorded the elevations of downstream distribution limits of Lahontan cutthroat trout in 19 streams without brook trout across northern Nevada in 1997 (Fig. 1). Data for an additional 11 streams were available from information on file with the Nevada Division of Wildlife, and Oregon Department of Fish and Wildlife.

Variable screening selected a two variable model with linear latitude and longitude effects (Table 1). Initially, the regression analysis was restricted to the 19 streams we surveyed in 1997. Overall, the OLS regression model explained over 67% of the variability in downstream distribution limits of Lahontan cutthroat trout. A regression of absolute values of studentized residuals in relation to predicted distribution limits from the model showed no relationship ($\underline{F} = 0.98$, $\underline{P} = 0.34$, $\underline{df} = 18$), indicating homogeneity of variances. Tests for normality of studentized residuals indicated model errors were normally distributed ($\underline{W} = 0.92$, $\underline{P} = 0.09$). The model predicted observations well, with PRESS residuals averaging 1.20 ± 114.55 meters of elevation.

Next, we extended the regression analysis to include all 30 streams for which data were available. The OLS model explained over 71% of the variability in downstream distribution limits. A regression of absolute values of studentized residuals in relation to predicted distribution limits from the model indicated heterogeneity of variances ($\underline{F} = 9.06$, $\underline{P} = 0.001$, $\underline{df} = 29$). This likely was due to the fact that surveys of distribution limits by agencies were concentrated in the northern and eastern portions of the range of Lahontan cutthroat trout (Figs. 1, 3). Model errors were normally distributed ($\underline{W} = 0.97$, $\underline{P} = 0.67$).

Inspection of influence diagnostics indicated that two streams in the Coyote Lake basin, the northern-most streams in our sample (Fig. 1), qualified as influential outliers (DFFITS < -0.63 or > 0.63), with DFFITS values of -0.73 and -0.95.

The presence of influential outliers and heterogeneous variances in the OLS model prompted us to conduct LAD regression using the full data set. Results of this analysis corroborated those obtained by OLS regressions (Table 1). As may be expected, there was some variability in the precision (width of confidence intervals) for parameter estimates among the three regression models (Table 1). In particular, the weaker effect of longitude ranged from marginally nonsignificant ($\underline{P} = 0.051$) in the original analysis of 19 streams to highly significant ($\underline{P} = 0.001$) in the OLS model of all 30 streams.

Streams with both Lahontan cutthroat trout and brook trout. Distribution limits for Lahontan cutthroat trout in streams with brook trout present were highly variable (Fig. 3) and not significantly related to latitude or longitude ($\underline{F} = 2.10$, $\underline{P} = 0.17$, $\underline{df} = 13$). A decreasing trend in the elevation of lower distribution limits, similar to streams without brook trout was evident, however (Fig. 3). The statistical significance of this trend was not changed by removal of an outlier data point from a stream with a translocated population of Lahontan cutthroat trout. On average, downstream distribution limits for Lahontan cutthroat trout in streams with brook trout were 226.79 meters higher in elevation than in streams without brook trout. This difference was highly significant (Wilcoxon rank-sum test, $\underline{P} < 0.0001$; see also Fig. 3).

Upstream distribution limits

Elevations of upstream distribution limits varied significantly as a function of latitude, longitude, and gradient. Analysis of covariance indicated barrier effects were not significant ($P = 0.13$). Upstream distribution limits varied most strongly as an inverse function of latitude ($P = 0.0001$) and gradient ($P = 0.002$), and less so as a positive function of longitude ($P = 0.01$). Upstream distribution limits were not related to stream size as measured by wetted stream width, maximum pool depth, or average depth. The model with latitude, gradient and longitude explained 61% of the variation in the elevation of upstream distribution limits. Values of studentized residuals and DFFITS did not suggest major problems with outliers or highly influential data points. Only three data points qualified as influential outliers (DFFITS < -0.61 or > 0.61); two (DFFITS = -1.00 and 0.65) from streams with a dispersal barrier (subsurface flow and waterfall, respectively) and one (DFFITS = -0.64) from a stream with no identifiable barriers. Regressions of absolute residuals indicated no problems with heteroscedastic errors ($F = 0.89$, $P = 0.45$, $df = 42$). The Shapiro-Wilk test indicated errors were not normally distributed ($W = 0.93$, $P = 0.01$), however. Log transformation of the data failed to remedy non-normality, but analysis of variance is robust to departures from this assumption (Underwood 1997), so we did not attempt further analyses. Correlation analysis (Table 2) revealed significant associations between maximum basin elevation and latitude, gradient, but not longitude. The strongest correlation ($r = 0.80$) was between maximum basin elevation and elevation of upstream distribution limit for Lahontan cutthroat trout.

Correspondence of downstream distribution limits to thermal gradients

We tested the fit of nine air temperature models to observed downstream distribution limits of Lahontan cutthroat trout. Each temperature model estimated the elevation corresponding to mean July air temperatures ranging from 16-24°C. Of the nine models, the data were best explained by the model corresponding to a mean July air temperature of 18°C (Fig. 4). The sum of squared deviations from model predictions of our latitude-longitude model (Table 1, model A) was 174,610 m^2, while the sum of squared deviations from the 18°C temperature model was 254,173 m^2. Squared deviations for the two next best models (19 and 17°C) were considerably larger, totaling 460,814 m^2 and 823,043 m^2, respectively (Fig. 4A). Predicted elevations of downstream distribution limits from climate models paralleled those predicted by our geographic model (Fig. 4B).

Discussion

We found major geographic gradients in the distribution of stream-living Lahontan cutthroat trout, with the notable exception of Lahontan cutthroat trout populations that co-occur with nonnative brook trout. In the latter case, a geographic gradient was not evident, and the distribution of Lahontan cutthroat trout was significantly reduced when brook trout were present. Geographic gradients in downstream distribution limits of Lahontan cutthroat trout were concordant with regional thermal gradients (Fig. 4B), but distribution patterns differed substantially from those predicted by recent climate models for salmonids in the Rocky Mountain region (Fig. 4A). Below, we discuss each of these results in more detail, with an emphasis on downstream distribution limits.

Downstream distribution limits

Changes in downstream distribution limits may have especially important implications for the productivity and viability of trout populations. In the basin and range physiographic province (Grayson 1993), which includes all of the eastern Lahontan basin, streams drain north-south trending mountain ranges, flowing into alluvial valleys with gentle slopes. As a result, the vertical profile of streams is generally j-shaped with higher gradient headwater reaches and lower gradient reaches downstream. Accordingly, an increase in the elevation of downstream distribution limits will result in a much greater loss of stream habitat, in terms of linear distance, in comparison to habitat loss from a decrease in the elevation of upstream distribution limits. Loss of downstream habitats also acts to increase the isolation of fish populations in headwater habitats, which may reduce the probability of population rescue or recolonization, and thus the probability of habitat occupancy (Rieman and McIntyre 1993; Dunham et al. 1997; Dunham and Rieman, in press).

Streams with Lahontan cutthroat trout only. In the absence of other salmonids, variability in the downstream distribution limits of stream-living Lahontan cutthroat trout populations was best explained by a model with linear latitude and longitude effects. Our model predictions were robust to the addition of distribution data collected in different streams and years (e.g. Table 1), suggesting distribution limits may be relatively constant, at least across the 20 year period over which distribution data were collected (1977-1997). Some fluctuation in distribution limits may be expected, however, as about 30% of the total variation is not explained by our model. A recent long-term study of brook and rainbow trout over a similar time period in east Tennessee streams similarly found no net change in distribution limits (Strange and Habera 1998). Future annual and seasonal monitoring of distribution limits will be needed to validate predictions of the geographic model proposed here, however.

Geographic variability in downstream distribution limits of Lahontan cutthroat trout closely paralleled regional thermal gradients. Previous work on climate variability in the region has shown July air temperatures to vary geographically, with colder temperatures in the north and warmer temperatures in eastern Lahontan basin (Mitchell 1976). This qualitative pattern corresponds well with patterns in the downstream distribution limit we observed for Lahontan cutthroat trout. The form of the regional model of mean July air temperatures developed by Keleher and Rahel (1996) differs somewhat from our models in that temperatures were predicted by a model with linear and quadratic latitude effects, and not longitude. In our regression analysis of distribution limits, we screened a quadratic model of the form used by Keleher and Rahel to predict regional air temperatures, but model selection criteria favored a linear latitude-longitude model.

We expected the downstream distribution limit of Lahontan cutthroat trout to correspond to geographically defined thermal limits as modeled by Keleher and Rahel (1996) and Rahel et al. (1996). These studies used trout distribution data from Wyoming Game and Fish Department surveys to establish a thermal limit corresponding to mean July air temperatures of 22-24°C. Our analysis of correspondence between distribution limits predicted by the regional Keleher and Rahel (1996) air temperature model and those observed for Lahontan cutthroat trout revealed, however, that downstream distribution limits corresponded most closely to a model assuming a mean July air temperature of 18°C, about 4-6°C cooler than generally expected for salmonids in the Rocky Mountain region.

Why do downstream distribution limits of Lahontan cutthroat trout correspond to such cooler air temperatures? One possibility is that Lahontan cutthroat trout are unusually intolerant of warm temperatures, but this is not supported by laboratory research (Dickerson and Vinyard, in press). A second possibility is that relationships between mean July air temperature, elevation and latitude may be unique in Nevada, and regional air temperature models developed by Keleher and Rahel (1996) may not apply. This seems unlikely as well, as Keleher and Rahel (1996) modeled an extensive 30 year (1951-1980) data base of air temperatures from 615 meteorological stations throughout the Rocky Mountain region, including Nevada. A more formal analysis of geographic patterns in air temperatures may be needed, however, to explore this alternative in more detail.

A third and related possibility is that air temperature-water temperature relationships in the study area are fundamentally different than for other parts of the region. It is possible that daily thermal maxima in the eastern Lahontan basin may exceed short-term preference or tolerance limits for Lahontan cutthroat trout, while mean temperatures remain within a suitable range. If such is the case, mean temperature may be less meaningful in terms of describing suitable thermal habitat. Variability or time of exposure to critical temperatures may be more important.

Another regional difference could be that many stream habitats in Nevada are relatively small in size. Accordingly, smaller scale climate influences also may be critical. On a local scale, air temperature-water temperature relationships can be profoundly influenced by topographic shading, and natural and human-caused variability stream channel morphology or riparian vegetation (e.g. Beschta et al. 1987; Platts and Nelson 1989; Armour et al. 1990; Li et al. 1994). Channel and riparian alterations by activities associated with livestock grazing and agricultural development are particularly evident in the Great Basin, including the eastern Lahontan basin (Platts and Nelson 1989; Platts 1991; Nelson et al. 1992; Coffin and Cowan 1995; Myers and Swanson 1995; Gutzwiller et al. 1997; Jones et al. 1998). It generally is believed such changes have elevated summer water temperatures in streams throughout the western United States, and increased temperature has been identified as one of the primary sources of water quality impairment affecting native salmonids in the Rocky Mountain region (see papers in Gresswell 1988; Young 1995; Duff 1996), and elsewhere (e.g. Meisner 1990a, b; Regier and Meisner 1990; Flebbe 1994; Eaton et al. 1995; Nakano et al. 1996).

In the preceding discussion, we have emphasized the potential influence of thermal gradients. Geographic gradients in geologic and/or geomorphic features of stream catchments could alternatively explain variability in downstream distribution limits observed for Lahontan cutthroat trout in this study (e.g. Nelson et al. 1992). It seems more likely, however, that thermal, geologic, and geomorphic conditions covary in the Lahontan basin, and may be interrelated. As streams flow from their headwaters high on mountain slopes through different geologic and geomorphic gradients (Nelson et al. 1992), they also become warmer as stream temperatures track corresponding increases in air temperature at lower elevations (e.g. Rahel et al. 1996). Geologic and geomorphic effects on surface and groundwater discharge also may be important (e.g. Baxter et al., in press). Further study of relationships among these factors is needed to more clearly resolve their direct and indirect relationships to downstream distribution limits of Lahontan cutthroat trout.

Finally, our analysis indicated water diversions did not significantly influence downstream distribution limits, suggesting they occurred near contemporary downstream distribution limits. In three southern streams with complete irrigation diversions, we observed Lahontan cutthroat trout using habitats at the point where water was shunted out of the channel, however, suggesting diversions were truncating downstream distribution limits to some degree. Obviously, downstream dewatering and diversions can have important impacts on fish populations by isolating upstream populations and constraining colonization and occupancy of downstream habitats, should such habitats be seasonally important dispersal corridors, or become suitable following habitat restoration, for example.

Influence of nonnative brook trout on downstream distribution limits. We found elevations of downstream distribution limits of Lahontan cutthroat trout to be significantly higher when brook trout were present. Other nonnative salmonids (brown trout, rainbow trout) were present in a few streams with brook trout, but these species occurred primarily in the lowermost reaches of streams, with brook and cutthroat trout occupying upstream habitats. In every case, brook trout occurred directly downstream of Lahontan cutthroat trout, which tended to be concentrated in upstream reaches. This is a typical pattern of segregation among brook trout and cutthroat trout (e.g. Griffith 1988; Fausch 1989;

Bozek and Hubert 1992), but specific mechanisms producing this pattern are not clear (Fausch 1988, 1989). More recent experimental evidence suggests temperature may play a role in upstream-downstream segregation of brook trout and Lahontan cutthroat trout (DeStaso and Rahel 1994).

Downstream distribution limits of Lahontan cutthroat trout in streams with brook trout did not follow the geographic patterns we observed for distribution limits in streams without brook trout. The fact that the presence of brook trout obscures potential geographic trends in downstream distribution limits is further evidence that brook trout may exert a strong effect on Lahontan cutthroat trout populations. The variability of this effect is large, however, and the distribution of Lahontan cutthroat trout in some streams seems scarcely affected, while in others the distribution is dramatically reduced relative to streams without brook trout (e.g., Fig. 3).

The large variability in the effect of brook trout on Lahontan cutthroat trout distribution suggests the possibility for habitat-specific interactions (sensu DeStaso and Rahel 1994; Harvey and Nakamoto 1997; Schroeter 1998). It also may be the case that variability in the timing of invasion by brook trout and dispersal barriers play a role in the contemporary downstream distribution of Lahontan cutthroat trout. Timing of invasion may be important in some cases, but stocking records for many streams indicate brook trout have coexisted with Lahontan cutthroat trout for several decades (P. Coffin, personal communication). Dispersal barriers to upstream migration of brook trout may be locally important, but we found obvious barriers in only three of 15 streams with both Lahontan cutthroat trout and brook trout.

headwater habitats may only be viewed as a short term strategy for population recovery/restoration, as such habitats are unlikely to support Lahontan cutthroat trout in the long term.

Stream gradient was positively correlated with upstream distribution limits, but also positively correlated with maximum basin elevation. The positive relationship between elevation of upstream distribution limits and stream gradient may therefore be an artifact of covariation between stream gradient and maximum basin elevation (as with longitude). Stream gradients at upstream distribution limits generally were greater than those associated with upstream distribution limits of Yellowstone cutthroat trout (O. c. bouvieri) (Kruse et al. 1997). Yellowstone cutthroat trout rarely occurred in stream habitats with gradients exceeding 10% (Kruse et al. 1997; see also Bozek and Hubert 1992), but stream gradients at upstream distribution limits in this study averaged 11.6%, ranging from 2.1 to 26.7% (Fig. 5). Results of this study suggest upstream limits of Lahontan cutthroat trout may simply be constrained by the maximum elevation of stream basins, and less influenced by steep gradients.

Conclusions. Patterns of distribution limits observed for Lahontan cutthroat trout in this study suggest important local and geographic influences, particularly for downstream distribution limits. On a local scale, it is clear that Lahontan cutthroat trout occupy less potentially suitable habitat when brook trout are present, but this effect is highly variable. The geographic model of downstream distribution limits for allopatric Lahontan cutthroat trout provided an important context for evaluating the effects of brook trout. On a geographic scale we were able to accurately predict the downstream distribution limit of allopatric Lahontan cutthroat trout populations in streams using only latitude and longitude as predictors, but we were not able to unequivocally determine causes of this relationship. Correlative evidence (see also Fig. 2) suggests thermal gradients likely play a role in determining downstream distributions, but other factors (e.g. geomorphology, geology) may play a direct or indirect role as well. Large discrepancies between predictions of more generalized climate-based distribution models for trout (Keleher and Rahel 1996) and downstream distribution limits we observed for Lahontan cutthroat trout point to the need for a better understanding of causal mechanisms. Such will require more detailed experimental and observational field study. Upstream distribution limits varied as a function of latitude and stream gradient, but effects of these variables were likely confounded with topographical variability within the region. Local influences (e.g. stream gradient, size, and barriers) seemed to matter less in terms of upstream distribution limits, suggesting Lahontan cutthroat trout may be relatively opportunistic in regard to selection of summer habitats in headwater streams.

Acknowledgments

This research was supported in part by the U.S.D.A. Forest Service Rocky Mountain (formerly Intermountain) Research Station (INT-96089-RJVA), and U.S. Fish and Wildlife Service, Region 1 (DOI-FW-1960007), with additional support from the Biological Resources Research Center, University of Nevada-Reno. Thanks to C. Carreno, G. Guscio, H. Miyagawa, M. Meeuwig, B. Prusha, S. Williamson, for long hours of field assistance, and to Nevada Division of Wildlife and Oregon Department of Fish and Wildlife for sharing data on distribution limits. Thanks also to R. Bamford for helping to produce Figure 1. Work on Lahontan cutthroat trout was authorized by Region 1 U.S. Fish and Wildlife Service and Nevada Division of Wildlife (permit nos. S-9039, S-0153, S-12357, S-14065, S-15425). Three anonymous reviewers and P. Connolly provided helpful comments on an earlier version of this manuscript.

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Table 1. Regression models of downstream distribution limits (elevation, in meters) of Lahontan cutthroat trout.

		Parameter			95% confidence interval	
Variable	df	Estimate	t	P	lower	upper
		A: UNR surveys, OLS regression				
CONSTANT	1	6716.13	7.33	0.0001	4773.45	8658.81
UTMN	1	-0.0011	-5.57	0.0001	-0.0016	-0.00071
UTME	1	0.00067	2.11	0.051	$-4.00 \cdot 10^{-6}$	0.0013
		B: UNR + Agency data, OLS regression				
CONSTANT	1	7579.17	8.46	0.0001	5740.97	9417.38
UTMN	1	-0.0014	-7.11	0.0001	-0.0018	-0.00098
UTME	1	0.00097	3.62	0.001	0.00042	0.0015
		C: UNR + Agency data, LAD regression				
CONSTANT	1	6675.60	8.31	0.0001	5026.49	8324.70
UTMN	1	-0.0011	-6.49	0.0001	-0.0015	-0.00077
UTME	1	0.00059	2.40	0.024	0.000086	0.0011

Table 2. Correlations (Pearson) between maximum basin elevation and "latitude" (UTM northing; UTMN), "longitude" (UTM easting; UTME), stream gradient (GRAD), and upstream distribution limits (elevation, in meters; ULIMIT) of Lahontan cutthroat trout. Values of correlation coefficients appear in the top row, while corresponding probabilities are displayed below.

	UTMN	UTME	GRAD	ULIMIT
Maximum basin elevation	-0.70	-0.003	0.36	0.85
	0.0001	0.98	0.02	0.0001

Figure captions

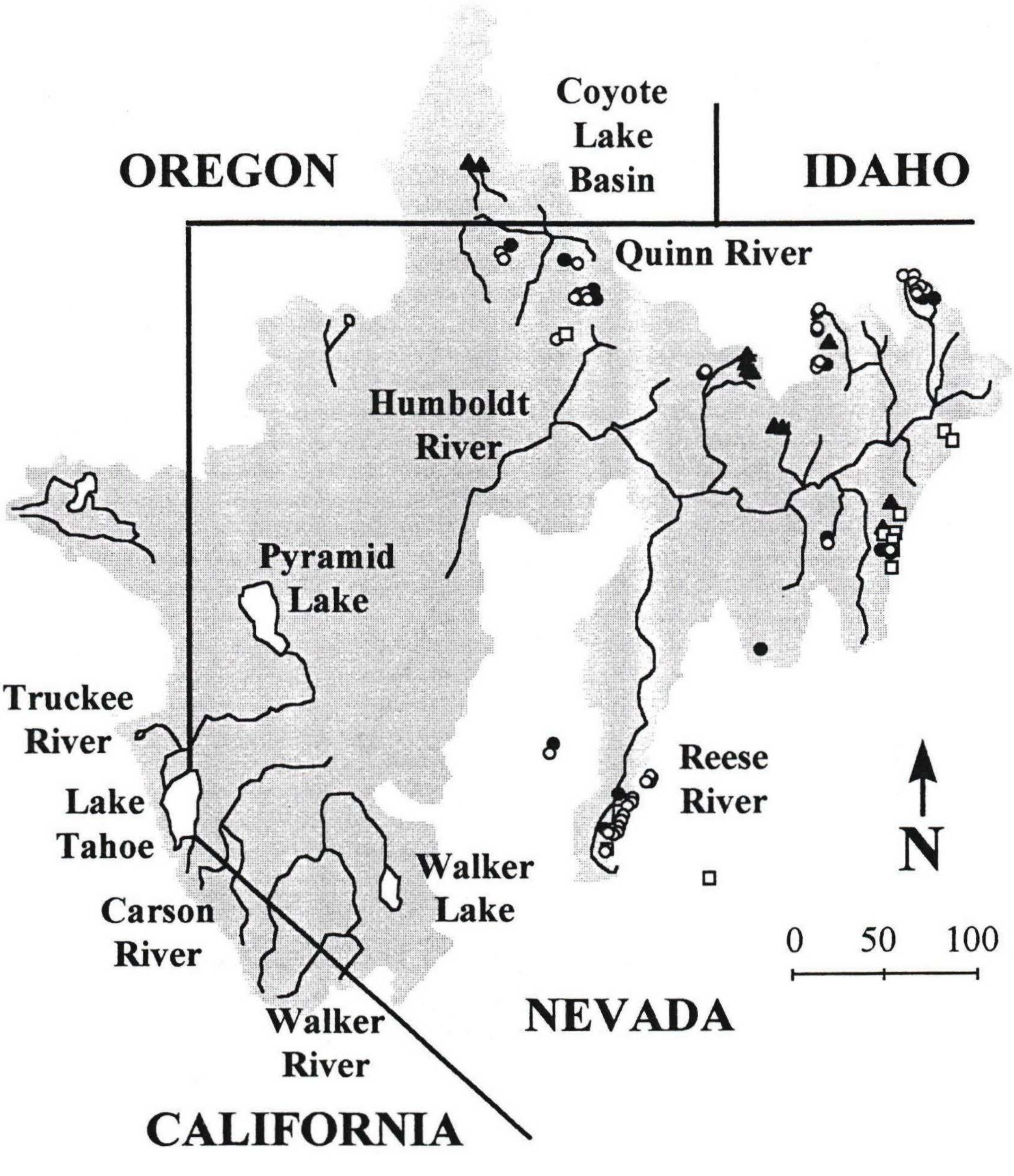
Figure 1. Map of Lahontan basin (shaded) with locations of streams sampled for up- and downstream distribution limits of Lahontan cutthroat trout. Note streams located outside of the basin are translocated populations. Symbols represent the following samples: ● = downstream distribution limits for streams with Lahontan cutthroat trout only; ▲ = downstream distribution limits for streams with Lahontan cutthroat trout only (agency data); □ = downstream distribution limits for streams with Lahontan cutthroat trout and brook trout; ○ = upstream distribution limits.

Figure 2. Longitudinal profile of maximum stream temperatures recorded (16 July - 15 September 1998) from Edwards Creek, Nevada (unpublished data). Filled and unfilled circles represent sites with and without Lahontan cutthroat trout present, respectively. Distance is an arbitrary measure of relative distance (meters) between sample sites, beginning with zero at the downstream site. The drop in maximum temperature at 1200 meters corresponds to the influence of discharge from a large, cold spring source.

Figure 3. Scatterplots showing elevation of downstream distribution of Lahontan cutthroat trout in streams of the eastern Lahontan basin (Fig. 1) in relation to latitude (UTM northings) and longitude (UTM eastings). Univariate regression lines are fitted to streams with only Lahontan cutthroat trout surveyed in 1997 (solid circles). Lines are fitted for visual reference only (see Table 1 for multiple regression results).

Figure 4. (**A**) Deviation between model predictions of elevations (m) corresponding to nine mean July air temperatures (Keleher and Rahel 1996) and observed elevations of downstream distributions of Lahontan cutthroat trout surveyed in 1997. The bar corresponding to "MODEL" refers to the sum of squared deviations for the best-fitting regression model of downstream distribution limits (model A, Table 1). (**B**) Plot of predicted elevations from three temperature models (18, 22, and 24°C) and MODEL in relation to latitude.

Figure 5. Distribution of stream gradients observed at upstream distribution limits.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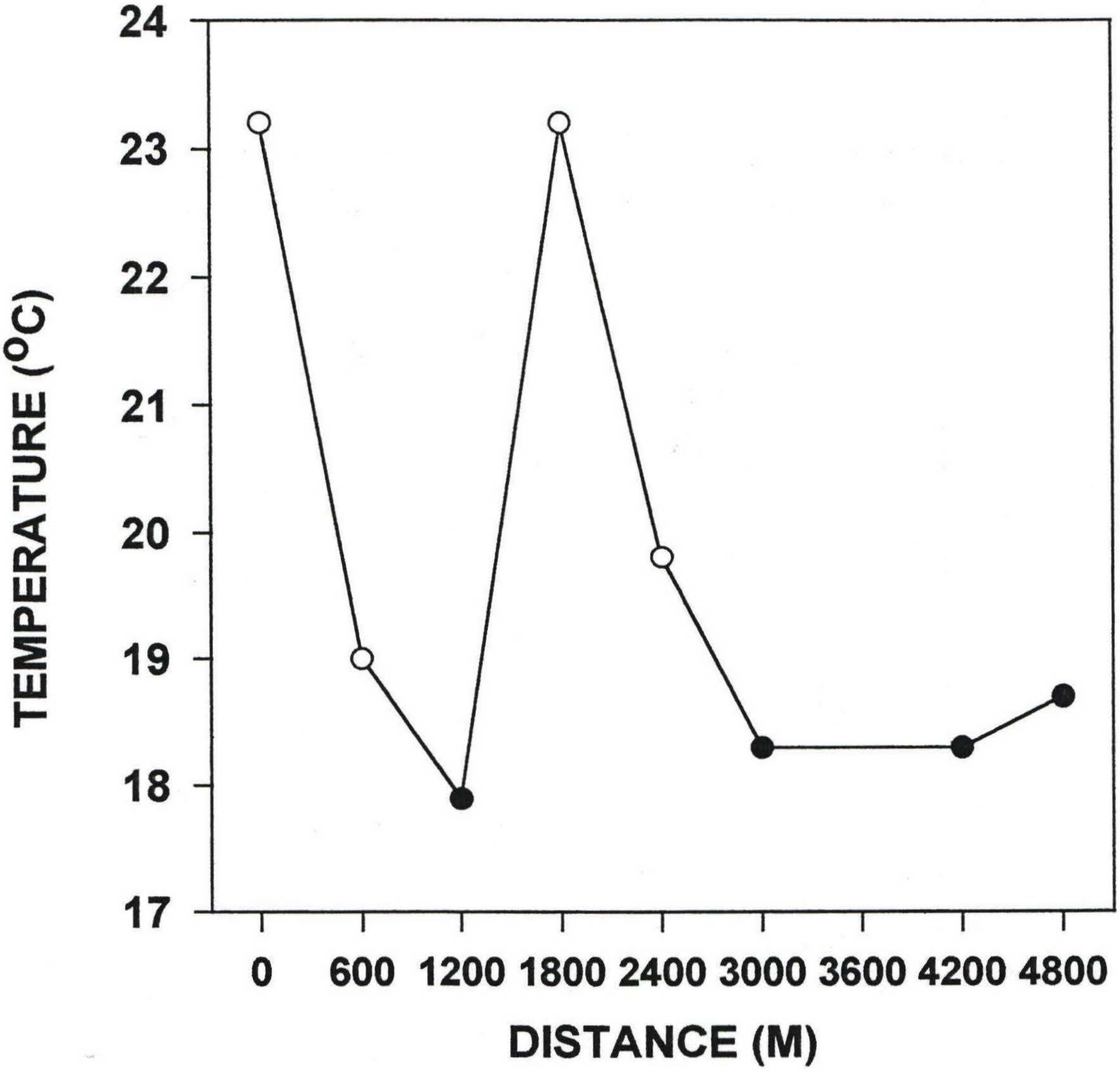
CALIFORNIA

F. . 1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23
22
21
20
19
18
17
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3000
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4200
4800
DISTANCE (M)

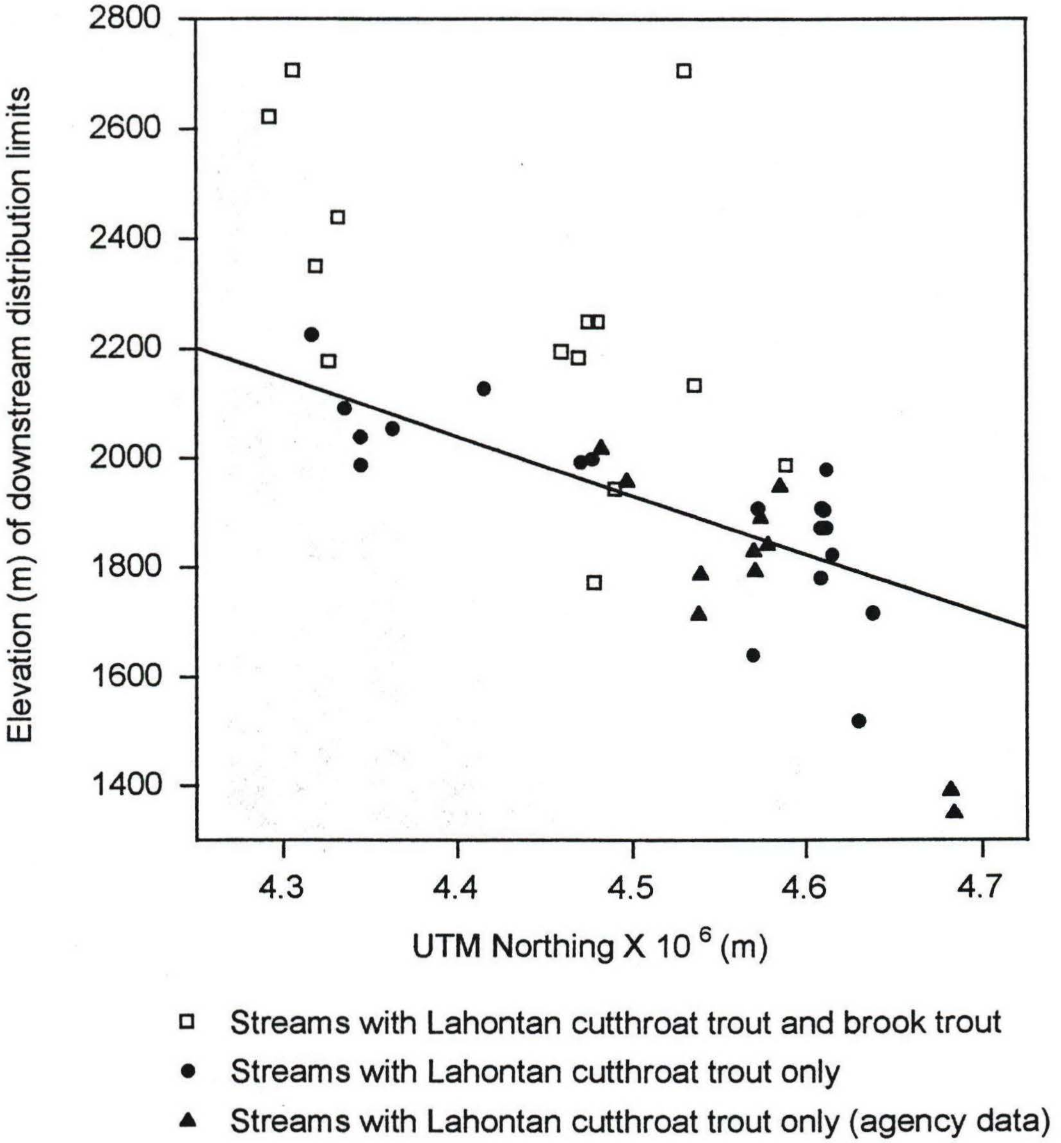
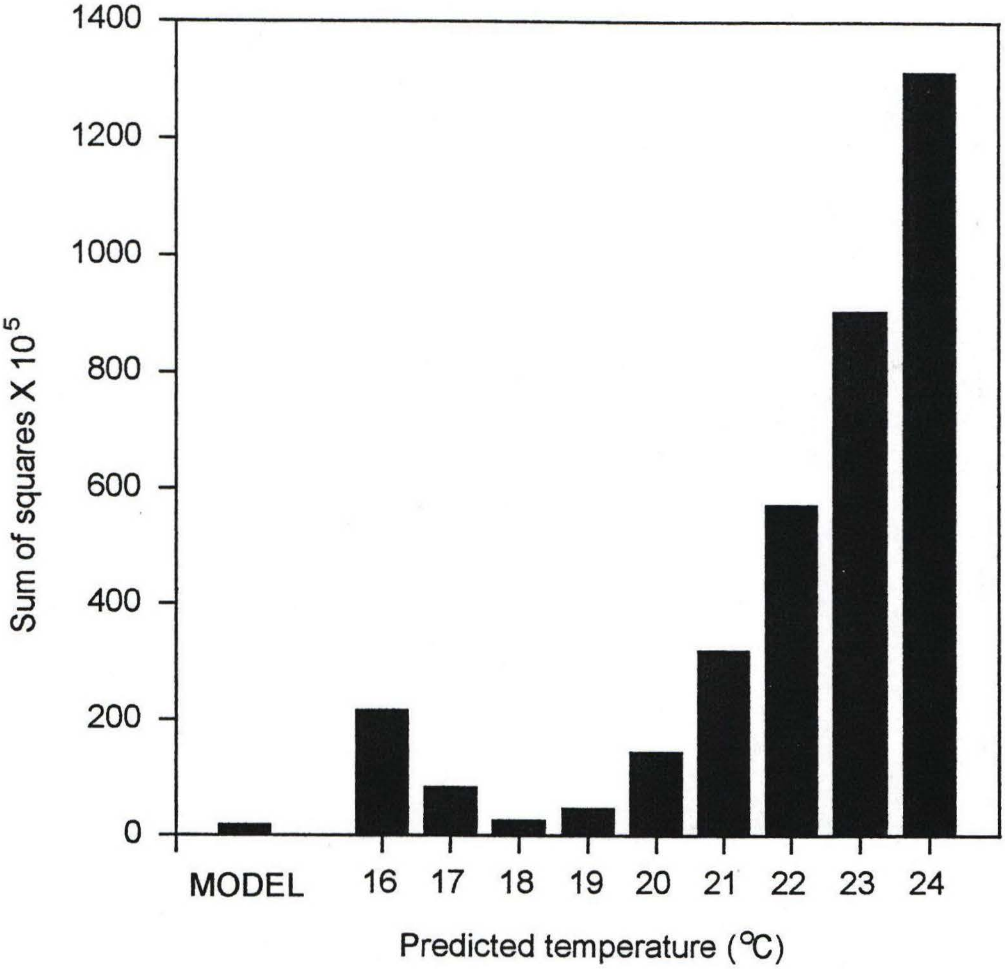

2800
2600
2400
2200
2000
1800
1600
1400
Elevation (m) of downstream distribution limits
4.3
4.4
4.5
4.6
4.7
UTM Northing X 10 ^{6} (m)
□ Streams with Lahontan cutthroat trout and brook trout
● Streams with Lahontan cutthroat trout only
▲ Streams with Lahontan cutthroat trout only (agency data)

Fig 3


1400
1200
1000
800
600
400
200
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Sum of squares X 10^5
MODEL
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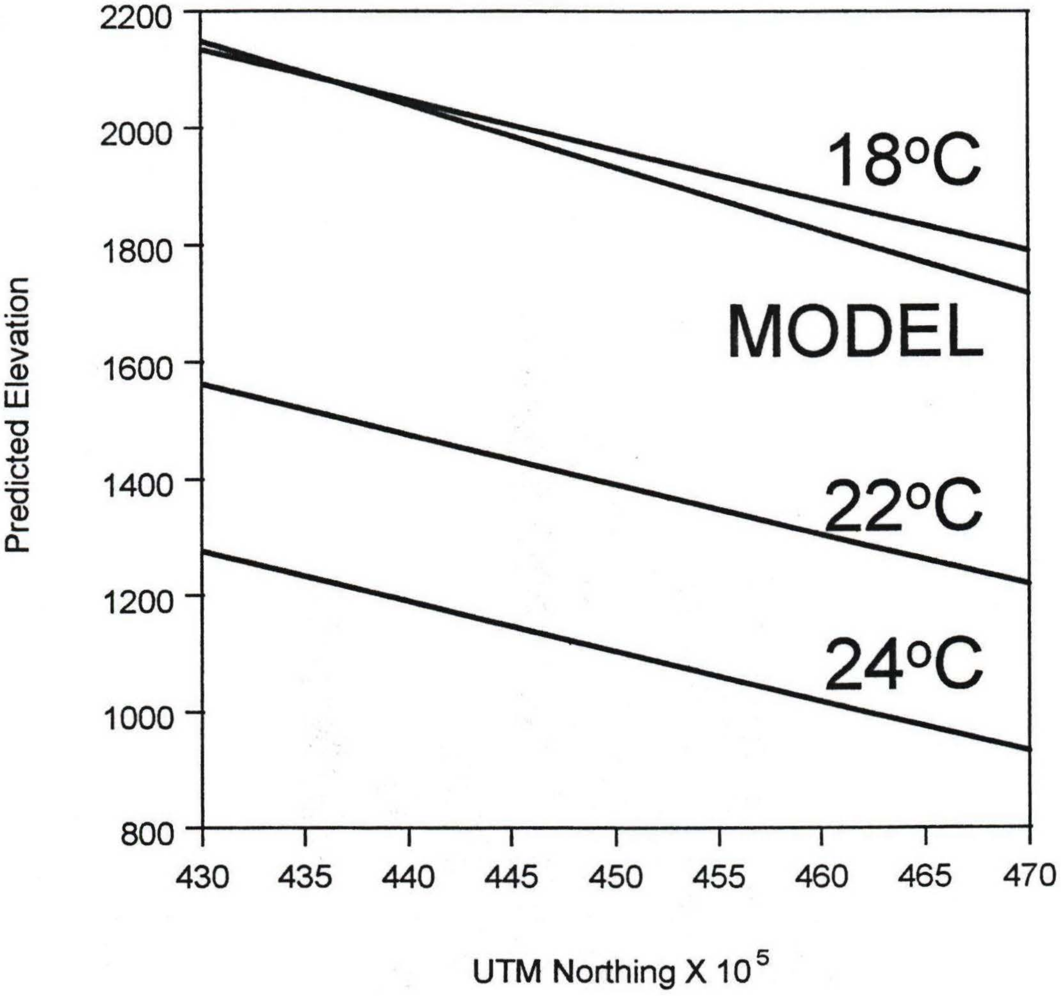
17
18
19
20
21
22
23
24
Predicted temperature (°C)


2200
2000
1800
1600
1400
1200
1000
800
Predicted Elevation
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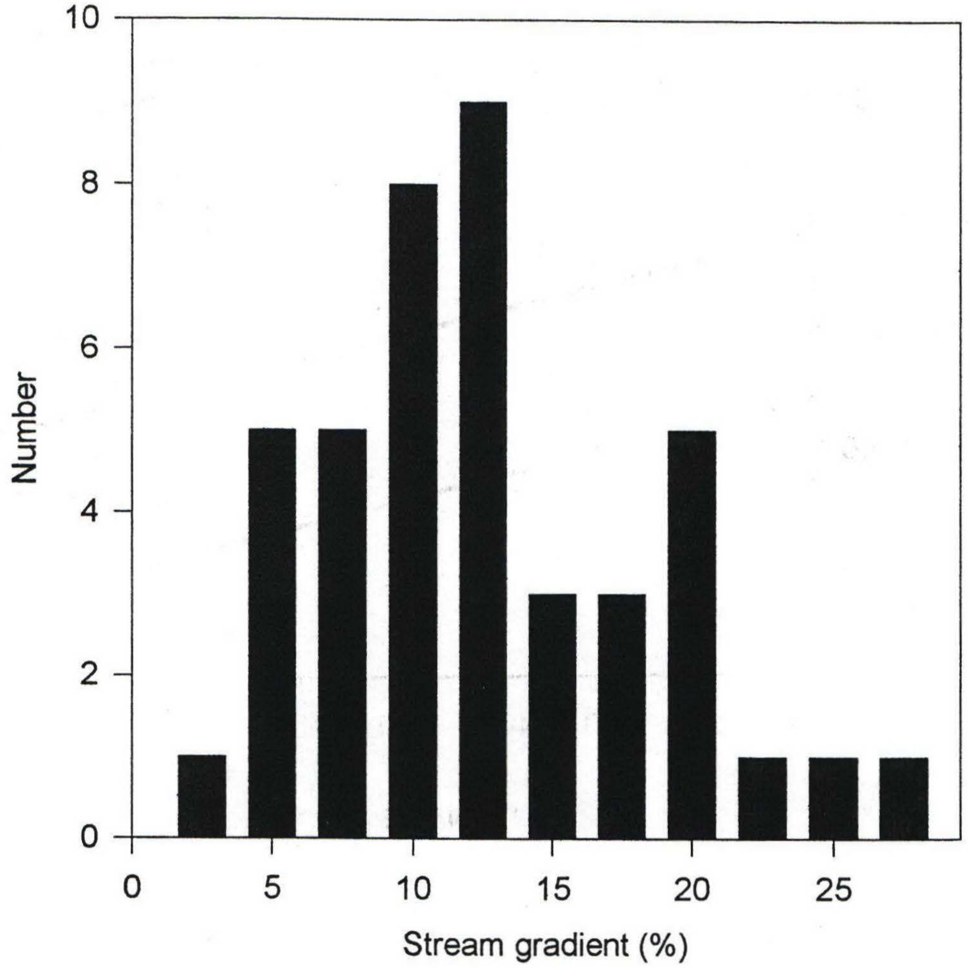
435
440
445
450
455
460
465
470
UTM Northing X 10⁵
18°C
MODEL
22°C
24°C


Number
10
8
6
4
2
0
0
5
10
15
20
25
Stream gradient (%)

Metapopulations and Salmonids: A Synthesis of Life History Patterns and Empirical Observations

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Key Words: salmonid, metapopulation, life history, dispersal, persistence, fragmentation

Suggested Running Head: Salmonid Metapopulations

Abstract- Metapopulation theory has attracted considerable interest with reference to the salmonids. There has been little empirical evidence, however, to guide the evaluation or application of metapopulation concepts. From knowledge of salmonid life histories and our own work with bull trout (*Salvelinus confluentus*) Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) we suggest that simple generalizations of salmonid metapopulations are inappropriate. Although spatial structuring and dispersal mechanisms are evident, the relevance of extinction and colonization processes are likely to vary with life history, species, scale, and landscape. Understanding dispersal, the role of suitable but unoccupied habitats, and the potential for extinction debts in non-equilibrium metapopulations are key issues. With regard to conservation of salmonids we suggest efforts to understand and conserve key processes likely to influence the persistence of populations or metapopulations will be more successful than efforts to design minimal habitat reserves based on metapopulation theory.

Introduction

Metapopulation theory has attracted considerable interest in conservation biology and management (Doak & Mills 1994; Hanski & Simberloff 1996). The proposal that regional populations of a species may persist in variable environments as collections of local populations interacting through dispersal (Hanski & Simberloff 1996) is intuitively appealing and has been largely embraced by biologists and managers (McCullough 1996). Metapopulation theory seems to hold a particular relevance for threatened or sensitive populations of salmonids in the Pacific

Northwest United States. It has been repeatedly invoked in recent discussions regarding conservation and land management relevant to these fishes (Rieman & McIntyre 1993; Bisson 1995; Li et al. 1995; Reeves et al. 1995; Schlosser & Angermeier 1995; Independent Scientific Group 1996; National Research Council 1996; Lee et al. 1997; Policansky & Magnuson 1998), although to date there has been little apparent direct application in land use management.

A metapopulation view implies that the spatial geometry (size, number, distribution) of suitable habitats matters to the dynamics and long-term persistence of these species' populations. Such issues may be particularly relevant for land managers that must decide about the priority of habitat or watershed conservation and restoration efforts (Doak 1995). How much habitat or how many watersheds are necessary; which ones; and how should they be distributed? Ostensibly, metapopulation theory should offer guidance for managers who face these issues (Rieman & McIntyre 1993; Li et al. 1995; Schlosser & Angermeier 1995). Conceivably, we might learn to identify a network of critical habitat reserves that would allow populations to persist in the face of ongoing development and disruptive land use.

Despite the interest there has been little empirical work to evaluate or guide the application of metapopulation theory to salmonids. Some authors caution that there are important risks of over-generalization and misapplication of intuitively appealing, but poorly supported theory (Simberloff 1988; Doak & Mills 1994; Hanski & Simberloff 1996). Unquestionably, large-scale processes have been important in the distribution and phylogeny of salmonid fishes in the Pacific Northwest. Current knowledge of local adaptation (E. B. Taylor 1991; Adkison 1995; National

Research Council 1996), zoogeography (McPhail & Lindsey 1986; McPhail 1997) and colonization of new habitats following introduction (Quinn 1993) or glacial retreat (Milner & Bailey 1989) clearly demonstrate the importance of spatial processes, environmental heterogeneity, and extinction-recolonization dynamics for these fishes. The question is not whether space is important; rather, how important is it (Karieva 1990)?

In an applied setting this question is constrained by the spatial and temporal scales of management decisions likely to influence these species. In our view the metapopulation question becomes most relevant at the scale of large watersheds or moderately sized river basins (10^2 to 10^3 km^2) where biological and socio-political processes overlap in a unique way. It is at this scale in the United States that land management is often controlled by a single or a few entities (e.g. U.S. Forest Service; Bureau of Land Management) charged with managing much, if not most, of an entire basin in a coordinated fashion. With the exception of the anadromous forms, it is at this scale that many of the salmonids fully express their life history potential (Northcote 1997; Thurow et al. 1997). Even forms that move more widely than the stream network encompassed at this scale are likely to use individual tributary systems within such an area as localized spawning and rearing areas. It is also at this scale that dams or habitat loss have created insular networks of habitats that now function as discrete units regardless of historical connections (Sheldon 1988; Lee et al. 1997).

In this paper we briefly review metapopulation theory. We then consider both the general knowledge of life history patterns, and recent empirical results for several salmonids as evidence of metapopulation dynamics. We conclude with a brief synthesis as guidance for further research and to identify the generalities and uncertainties relevant to the application of metapopulation concepts for salmonids.

Metapopulation Theory

The concept of spatially structured populations is not new, but the formalization of metapopulation theory has advanced dramatically in the last decade (Hanski & Simberloff 1996). In the classic view, metapopulations were considered collections of roughly equivalent demes or local populations with similar, but independent risks of extinction through environmental variability. In the simplest models and subsequent extensions, local extinctions are balanced by migration and recolonization from the extant populations (Hanski & Simberloff 1996; Harrison & Taylor 1996; Hanski 1997).

Metapopulation models have been extended to consider a variety of more complex systems. These may include substantial variation in the characteristics and dynamics of local populations and the patterns and rates of dispersal among them (Hanski & Simberloff 1996; Harrison & Taylor 1996). In the current view three conditions define metapopulations: 1) habitat consists of discrete patches or collections of habitats capable of supporting local breeding populations; 2) the dynamics of occupied patches are not perfectly synchronous; 3) dispersal among the component populations influences the dynamics and/or the persistence of the metapopulation or at least some of the local populations. Structuring and at least partial independence of local populations are the fundamental concepts that distinguish a metapopulation from a simple panmictic group in a patchy environment.

In reality, conformity to these conditions will vary across temporal and spatial scales, species, and landscapes. Harrison & Taylor (1996) conceptualized this variation as a continuum along two axes (Fig. 1). One axis represents relative dispersal among patches. The second represents variation or heterogeneity in patch quality which includes patch size or other characteristics likely to influence the size and dynamics of local populations.

At one extreme, relatively high rates of dispersal lead to high levels of recolonization and patch occupancy, yielding a "patchy" population structure. If rates of dispersal and/or recolonization are very low, a non-equilibrium metapopulation structure may result. Non-equilibrium refers to a progressive pattern of local extinctions that occurs when rates of extinction exceed recolonization, such that patch occupancy ultimately declines to zero.

If variation in patch quality is high, some local populations may be relatively resistant to extinction, whereas others may be extinction-prone. This type of structure is often referred to as "mainland-island," where the largest local populations (defined in terms of population size or patch area) or "mainlands" are key to persistence of the metapopulation. Smaller "island" patches have relatively high rates of turnover, due to higher rates of local extinction and recolonization from mainland patches.

Harrison and Taylor (1996) noted that variability in habitat quality, rather than patch or population size, may produce a similar structure. In this context quality may be defined as the capacity of a patch to support populations with positive rates of growth. Patches with negative growth rates often are referred to as "sinks" (Pulliam and Danielson 1991; Dias 1996). Persistence of local populations in sink habitats depends on immigration of individuals from "source" habitats. In practice, mainland-island and source-sink structures may be difficult to distinguish (Dias 1996).

When variability in patch quality is low, and dispersal and/or recolonization probabilities are "just right," patch occupancy will approximate the dynamics of a classic or "Levins-type" metapopulation, where even the largest patches have a substantial risk of extinction, but no patches are too isolated to be recolonized (Hanski 1996; Hanski & Simberloff 1996). Though important for some species, this type of metapopulation structure may be rare in nature (Hanski 1996; Harrison & Taylor 1996).

There have been a variety of methods used to study metapopulations, each with unavoidable limitations. The application of multiple and complementary sources of information, however, can provide a more rigorous descriptive and quantitative understanding (Utter et al. 1993; Dunham et al., In Press a). Common approaches have included the analyses of distributions, population dynamics, and genetic structuring.

Patterns in species distributions have proven particularly useful. A general approach has been to describe the geometry of suitable habitat patches and then inventory those patches to describe patterns of occupation. Incidence functions (B. L. Taylor 1991; Hanski 1997) have been used to model the probability of species presence or persistence in relation to patch characteristics. This approach, often focused on patch area effects (B. L. Taylor 1991), has been used to estimate extinction and colonization rates as well. The latter application requires an assumption of an extinction-colonization equilibrium (Hanski 1997), or a time series of observations of extinction and colonization events (Ouborg 1993; Sjögren-Gulve & Ray 1996). Even when data are limited to a simple snapshot in time and an assumption of equilibrium is not justified, incidence functions can provide valuable insight regarding the patch characteristics associated with a species' occurrence and persistence. Incidence functions have been widely applied (see Hanski 1997), but applications with fishes are limited and presently we are familiar only with our own attempts with salmonids (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman, In Press).

Analyses of population dynamics and demographics have played a central role in the development of metapopulation concepts. Spatially detailed demographic models have been widely used in theoretical exploration of metapopulation dynamics (e.g. Fahrig 1992, 1997). There has been a more limited application to specific metapopulation questions, presumably because parameterization of such models can be extremely difficult (Doak & Mills 1994; Taylor 1995; Ims & Yoccoz 1996; Mills et al. 1996; Ruckelshaus et al. 1997). That does not mean demographic models are not useful. Patch-specific models can provide important tests of the common assumptions in metapopulation models (Ims & Yoccoz 1996); for example, to determine whether local populations are internally self sustaining or likely dependent on outside demographic support (e.g. Stacey & Taper 1992). Recent work with salmonids has focused generally on the dynamics of individual populations (e.g. Lee & Hyman 1992; Emlen 1995; Ratner et al. 1997; Shepard et al. 1997; Botsford & Brittnacher 1998).

Patterns of molecular genetic variation may reflect underlying processes of gene flow and dispersal and have been employed to characterize potential metapopulations (Driscoll 1998; Saccheri et al. 1998). Molecular genetic markers have been widely applied in the analysis of salmonid distributions (Allendorf & Waples 1995) but direct inferences regarding metapopulation dynamics have been relatively recent (e.g. Tallmon 1996; Fontaine et al. 1997; Spruell et al., In Press *this volume*).

Metapopulations and Salmonids

Salmonids would seem prime candidates for metapopulations. The spatial discreteness of spawning and rearing habitats, combined with the possibility of among-habitat dispersal, effects of local environmental variability, and disturbance regimes may create a patch dynamic that can be described by metapopulation models (e.g. Rieman & McIntyre 1993, 1995; Li et al. 1995; Reeves et al. 1995; Schlosser & Angermeier 1995; Dunham & Rieman, In Press). Well-known patterns of natal homing (Quinn 1993; National Research Council 1996) and local adaptation (E. B. Taylor 1991; Utter et al. 1993; Allendorf & Waples 1995) may reinforce structuring of local populations. Periodic straying among natal streams also is well known (Larkin 1981; Labelle 1992; Quinn 1993; Tallman & Healey 1994), however, providing a mechanism for dispersal.

Coupled with the knowledge that salmonid numbers may vary and that local extinctions have occurred or are more likely with increasing habitat loss and fragmentation (e.g. Rieman & McIntyre 1993; Dunham et al. 1997), this basic understanding has prompted repeated reference to metapopulation theory. The evidence seems compelling and salmonid metapopulations are sometimes taken for granted (Policansky & Magnuson 1998).

While it is clear that a metapopulation view of salmonids may be appropriate, the details of metapopulation structure and dynamics may depend critically on the large-scale structure of habitats, and how habitat and life history variability interact (Dunham & Rieman, In Press). If metapopulation theory is to be meaningfully applied to salmonids, such issues must be considered in some detail. General knowledge of salmonid life history patterns and recent empirical work provide a foundation from which to start.

Life History

Metapopulation structure is a function of quality, spatial distribution, and isolation of habitat patches (Fig. 1). Quality and distribution of potential patches can be defined as a function of physical factors including habitat size and condition, and biotic factors including habitat requirements and the modifying effects of other species. Isolation is a function of distance between patches, the nature of the intervening environment, and rates of dispersal (Wiens 1996). The term "straying" is often used in place of dispersal (Quinn 1993). We use both terms in this paper. Straying implies that an individual is lost, although it still may reproduce outside its natal habitat. Dispersal implies movement with the potential for colonization or demographic support of other patches. While straying may limit individual reproductive success (e.g. Tallman & Healey 1994), it is necessary for dispersal in salmonids and we wish to avoid the implication that it is maladaptive (see Cury 1994; LePage & Cury 1997).

Definition of patches, their distribution, and isolation, can depend strongly on the life history of the species in question. Migratory behavior may be particularly important in this regard. There is little question that migratory individuals can move the distances required to disperse among tributaries. Straying among tributaries obviously occurs, but straying and dispersal rates are poorly known (Quinn 1993). There is evidence that dispersal varies among species and with the particular circumstances of the species and systems in question (Quinn 1993; Quinn & Unwin 1993; Tallman & Healey 1994).

The salmonid literature is rich with examples of life history variability (see for example E. B. Taylor 1991; Groot & Margolis 1991; Northcote 1997; Willson 1997). Available evidence suggests three general patterns of migration for salmonids: migratory, resident, and mixed (resident + migratory individuals in the same populations). These categories may be further divided into "obligate" and "facultative," depending on the relative influences of genetic and environmental factors, respectively, on migratory behavior.

From a metapopulation perspective, the distinction between obligate and facultative migratory behavior may be important. Examples of obligate migratory behavior are provided by several species of Pacific salmon (e.g. *O. gorbuscha, O. keta, O. tshawytscha, O. kisutch*). These species are almost exclusively anadromous; adults that mature in freshwater (if present at all) are primarily precocial males (Groot & Margolis 1991; Stearley 1992). Individuals of these species require several spatially discrete habitats for different portions of their life cycle (e.g. upstream spawning and rearing habitat, downstream migration corridors, estuary and marine feeding habitats). Habitats used by salmonids with obligate migratory behavior are non-substitutable in the sense that different stages of the life cycle must occur in specific habitats (see Dunning et al. 1992; Schlosser 1994). Loss of any specific habitat required for a critical life stage will therefore result in extinction of associated local breeding populations. An unfortunate example of non-substitutability is recent extirpation of Pacific salmon in many habitats where migration barriers have been placed between upstream spawning and rearing habitats and downstream migration corridors and critical feeding habitats (Lee et al. 1997).

Many salmonids exhibit flexibility in their use and substitution of habitats (Northcote 1997). An excellent example is provided by sockeye salmon (*O. nerka*), where local populations of resident, fluvial, or lacustrine individuals may co-occur with anadromous individuals (Burgner 1991; Wood 1995). Individuals with different migratory life histories may occasionally interbreed (e.g. Taylor et al. 1996; Wood & Foote 1996), but each life history type can function independently. In the case of sockeye salmon, many anadromous populations have been decimated by degradation of migration corridors and lack of passage over dams (Lee et al. 1997), but resident populations of kokanee salmon have persisted. Resident forms may even produce anadromous offspring (Rieman et al. 1994).

For some species and populations of salmonids, movements of individuals are largely restricted to headwater stream habitats, where distributions of adults, juveniles, and spawning habitats overlap considerably. Such resident ("non-migratory") populations have been observed for bull trout (*Salvelinus confluentus*), where unsuitable thermal habitat may isolate headwater populations (Rieman & McIntyre 1995). Occurrence of downstream populations of predators or competitors (especially nonnative salmonids) has also been hypothesized to be an isolating mechanism that may promote residency (Fraser et al. 1995; Dunham & Rieman, In Press). Resident populations may occur upstream of more obvious barriers, including impassable waterfalls (Northcote 1992) and dams (Näslund 1993). In this latter example, opportunities for development of metapopulations are limited as recolonization of above-barrier habitats is not possible.

Migratory behavior of salmonids can have important implications for the degree to which the dynamics of local populations covary within a metapopulation. In the case where most adults undergo extensive migrations, habitats used for spawning and early rearing may be distributed as discrete patches throughout a drainage basin but migratory juveniles and adults may coalesce downstream. Use of these common habitats may act to link dynamics of local breeding populations. For example, decadal cycles in marine productivity can produce correlated dynamics of salmonid populations that spend their adult lives in common oceanic domains (Pearcy 1997).

On the other hand, environmental variability and disturbance in upstream spawning and rearing habitats may decrease the degree to which local populations covary (Reeves et al. 1995; Rieman & McIntyre 1996). Even when most individuals in a system may be migratory, variability of time spent in feeding habitats, timing and distance of migrations, and spatial and temporal overlap of spawning and rearing (E. B. Taylor 1991) may affect the degree of synchrony among local breeding populations.

For species and systems where migratory behaviors are more flexible (i.e. "facultative"), additional complexity is added by interactions between resident and migratory individuals (as with sockeye salmon and kokanee). Species with primarily resident populations may have a much restricted or even nonexistent interaction dynamic among local populations.

Our overview of salmonid life histories implies a potential for complex interactions between life history diversity and the structure and dynamics of metapopulations. While the evidence for salmonid metapopulations seems compelling in some cases, specific empirical studies are sorely lacking for salmonids and freshwater fishes in general (Schlosser & Angermeier 1995). In the following section, we review examples of recent empirical work, focusing on three inland salmonids that have been the subject of our own research. With regard to our discussion of life history complexity in the previous section, these examples are limited in that complexities posed by contrasting life histories are not fully addressed. Even so, we find evidence of very different patterns among these species.

Empirical Evidence

Bull Trout- Bull trout (*Salvelinus confluentus*) can be found virtually anywhere in the network of streams in river basins of at least sixth order. Some individuals can move hundreds of km (Bjornn & Mallet 1964; Swanberg 1997) while others remain within a local stream network throughout life. Bull trout have an indeterminant life cycle with first maturity occurring roughly between ages 3 to 6 with the possibility of subsequent repeat spawning (Fraley & Shepard 1989).

The distribution of resident and juvenile migratory bull trout is strongly associated with gradients in stream size and elevation or local climate (Rieman & McIntyre 1995; Rich 1996; Dunham & Rieman, In Press). Natal habitats are restricted to headwater streams as discrete patches in a matrix of the larger stream network representing an entire river basin (Fig. 2). Topography and hydrologic development interact with climate to create a mosaic of patches that can vary in size and isolation by stream distance among those patches (Dunham & Rieman, In Press). Because spawning is not known in lakes, populations associated with tributaries of lake systems may be structured similarly even when gradients in stream size and local climates are not large. These patterns indicate that spatially discrete local populations of bull trout are likely to exist in river basins as small as 10^2 km^2. Genetic analyses provide supporting evidence of homing and population structuring at this scale (Kanda et al. 1997; Spruell et al., In Press *this volume*).

Rieman & McIntyre (1995) found the occurrence of bull trout in the Boise River basin, Idaho to be strongly associated with the size (catchment area) of the habitat patches described in Fig. 1. Dunham & Rieman (In Press) analyzed an expanded data set and found both patch size and isolation (stream distance to nearest occupied patch) were strongly associated with the occurrence of bull trout. Variability in the size and distribution of patches within the basin suggested metapopulation structure was a complex mosaic of several elements found in conceptual models (Fig. 1). Potentially confounding effects such as spatial autocorrelation linked to undescribed environmental variability did not appear to be important. Human disturbance (as indicated by road density), however, was negatively correlated with occurrence.

Some of the best demographic information available for bull trout comes from annual redd counts (a measure of adult population size) for a number of tributaries associated with the large lakes of northern Idaho and Montana. Rieman & McIntyre (1993) used the analytic models proposed for time series by Dennis et al. (1993) to estimate the extinction parameters for these populations. They estimated that few could be expected to persist for an extended period (i.e. 100 years), if it was also assumed that each population existed in complete isolation. Other analyses of related data showed that interannual variation in adult number was not strongly correlated among tributaries, but there did appear to be a general pattern of decline across many of these populations (Rieman & McIntyre 1996; Rieman & Myers 1997). If these populations have always been at risk of extinction then dispersal among populations is necessary to explain their existence. Because a few very large and stable populations are found in these systems (Rieman & McIntyre 1993), source-sink or mainland-island metapopulation structures are logical alternatives.

Genetic analyses provide a different perspective. Phylogenetic work suggests an historical pattern of periodic contraction and local extinction followed by expansion and colonization from local refugia has been important across the species' range (Leary et al. 1993; Williams et al. 1997). Analyses of fine scale (i.e. within a river basin) genetic variation and divergence, however, suggest patterns that are not consistent with either the frequent extinction-colonization dynamic of a classic metapopulation structure or the source-sink possibilities suggested by the demographic data (Tallmon 1996; Spruell et al. In Press *this volume*).

Lahontan Cutthroat Trout- In contrast to bull trout in the Boise basin, distribution of suitable habitat for Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) has been dramatically reduced by habitat degradation, especially that related to increased water temperatures and migration barriers, and nonnative salmonids (Coffin & Cowan 1995; Dunham et al. 1997). It is estimated that Lahontan cutthroat trout has been extirpated from almost 90% of over 5700 km of formerly occupied stream habitats in the Lahontan basin of northeast California, southeast Oregon, and northern Nevada (Coffin & Cowan 1995). Most populations of Lahontan cutthroat trout exist as isolated enclaves in headwater stream habitats within the Humboldt and Quinn River basins of Nevada and Oregon. Historically, most of these habitats were interconnected via larger downstream river habitats that are no longer occupied (Coffin & Cowan 1995).

Analysis of factors associated with contemporary distribution limits of Lahontan cutthroat trout (Dunham et al., In press b) has produced a predictive model that can be used to estimate patch size and isolation. Over 70% of the variation in the elevation of downstream distribution limits for Lahontan cutthroat trout in streams was explained by latitude and longitude alone. This pattern was related to regional thermal gradients, and Dunham et al. (In press b) hypothesized that patch structure may be a function of suitable thermal habitat in streams, a factor that appears to explain bull trout distributions as well (see above). Relationships between water temperature and the distribution of Lahontan cutthroat trout within streams (JBD, unpublished data) further supports this hypothesis.

Persistence of Lahontan cutthroat trout in streams appears to be strongly tied to fragmentation of habitat. Dunham et al. (1997) analyzed occurrence of Lahontan cutthroat trout in 119 stream habitats in the Humboldt and Quinn River basins of northern Nevada. They found a strong negative association between occurrence of Lahontan cutthroat trout and fragmentation of habitat. Due to uncertainties in defining the distribution of suitable habitat within streams, they could not clearly distinguish the effects of habitat size and isolation. An improved definition of patch structure based on recent distribution models (Dunham et al., In press b, and unpublished data) will be used to revisit this analysis to quantify the individual effects of patch size and isolation.

Observations on apparent local extinctions of Lahontan cutthroat trout in small tributary streams following catastrophic drought conditions in the early 1990s (Dunham 1996) offer additional insights into the relevance of isolation and life history diversity to population persistence. Following the drought, recolonization in isolated streams was never observed. Tributaries with close proximity to a larger river, however, often were quickly (within 1 yr) repopulated. In the latter case, it was not clear whether restoration of fish distributions was through surviving members of the population that had migrated out of the tributary during the drought or through dispersal from another population. Similar patterns of recolonization in tributaries or stream sections have been observed with other salmonids following catastrophic disturbances (Rieman et al. 1997).

Westslope Cutthroat Trout- Work with westslope cutthroat trout (*Oncorhynchus clarki lewisi*) is preliminary but offers an interesting contrast to that emerging for the other two species. The distribution of westslope cutthroat trout also has been strongly associated with stream size (Platts 1979). Although westslope cutthroat trout may move throughout whole river basins, at least temporarily occupying habitats from second through sixth or seventh order streams (Bjornn & Mallet 1964), spawning and initial rearing has been linked primarily to the smaller tributaries (Johnson 1963; Fraley & Shepard 1989). Dunnigan (1997) found that age 0 cutthroat trout in the Coeur d'Alene River basin of Idaho were generally restricted to first to third order streams. The distribution may be a response to availability of suitable habitats, predation, or the influence of spring stream flows and patterns of scour (Johnson 1963; Lukens 1978; Dunnigan 1997). In any case, the pattern indicates spatial structuring of westslope cutthroat trout populations is also likely within river basins of a few hundred km^2.

The numbers of subadult and adult cutthroat trout observed in the mainstem rivers of the Coeur d'Alene basin declined to very low levels in the last 30 to 40 years (Lewinsky 1986). Because fish in the larger rivers are believed to be the migratory representatives of local populations associated with individual tributaries, the decline might represent an important loss of the potential for dispersal among those populations.

Working with collaborators we hypothesized that if cutthroat trout in the Coeur d'Alene basin functioned as a metapopulation, extinctions among tributary populations would be more pronounced with increased isolation. Dunnigan (1997) found that the network of streams representing tributary patches often supported very low densities of cutthroat trout. Extrapolations based on available habitat indicates that many local populations must number fewer than 200 total individuals (BER, unpublished data). Despite the small size of these populations, three years of inventory including more than 90 tributary systems produced no evidence of a local extinction (i.e. all surveyed streams were occupied in all years). In 1996 following a large winter flood (approximately 100 year return interval, Beckwith et al. 1996), we resurveyed more than 50 tributaries and again found no evidence of local extinctions.

The persistence of tributary populations of cutthroat trout in this system may be explained in two ways. First, extinction and recolonization occurs very quickly (i.e. patchy population). Alternatively, even very small populations of westslope cutthroat trout are not prone to extinction through environmental variation on the scale we have considered. Analysis of genetic structuring among these tributary populations may provide a test of these alternatives. The absence of fish in the mainstem, however, and the persistence of westslope cutthroat trout in numerous small streams isolated by natural and human caused barriers (BER, unpublished data) support the latter alternative.

Discussion

The empirical evidence does not support a generalizable model of metapopulation dynamics for inland salmonids. The basic elements of spatial structuring and dispersal almost certainly are present in many systems, but the dynamics of these populations don't appear to be simple or consistent. Although much of the emerging information is consistent with metapopulation processes, those results can be interpreted in a variety of ways.

For example, the current demographic and distribution patterns may be recent (in ecological time) results in changing systems. Both Lahontan cutthroat trout and bull trout were more likely to be found in large or interconnected habitat patches. From that we suggest that local extinctions are more likely in small or isolated patches. That pattern is consistent with an extinction-colonization equilibrium, but we cannot exclude a second alternative: a regional decline or non-equilibrium system (Harrison & Taylor 1996), where the large or closely interconnected patches are simply the last to go extinct. Both Lahontan cutthroat trout and bull trout have declined throughout a large portion of their historical ranges. The condition of local habitats has been degraded and fragmentation has been aggravated by human related disturbance (Rieman & McIntyre 1993; Coffin & Cowan 1995). We simply cannot be certain whether we are observing evidence of a metapopulation dynamic characterized by a balance between extinction and recolonization, or a deterministic slide toward growing local and regional extinctions (Doak & Mills 1994; Hanski & Simberloff 1996).

Our understanding of salmonids and metapopulations is constrained by the spatial and temporal scales over which they can be, or have been studied. Evidence that some local populations are prone to extinction without demographic support from neighboring populations does not mean that dispersal has been important in stabilizing the system. Genetic information for some bull trout populations, for example, suggests dispersal has been limited (Spruell et al., In Press *this volume*). Alternatively, evidence of limited extinction and colonization in the past also does not mean these processes will not be important in the future. Conceivably, the loss and fragmentation of habitats can accentuate metapopulation processes where they were less important before. If dispersal is strong enough, a metapopulation dynamic may emerge in mosaics of remnant habitats.

It is important to consider that dispersal and straying rates probably are not stable through time but occur as punctuated events or vary with population densities, the degree of local adaptation, and the disruption or condition of local habitats or migratory corridors (Quinn 1993; Quinn & Unwin 1993; Walters 1997). Over longer time scales, variability in rates of dispersal may result as distributions of some species track long-term trends in habitat availability and suitability. For example, the geometry of bull trout habitats is apparently influenced by climate. The current distribution of bull trout may reflect relatively recent climatic variation occurring on decadal scales (e.g. Pulwarty & Redmond 1997) or longer term expansion and contraction of habitat associated with the cooling and warming trends of the last several centuries (Stine 1996).

Given enough time and a source of colonists, expansion of populations into suitable habitats across whole river basins would seem almost certain for most salmonids. Whether dispersal can occur quickly enough or in the numbers necessary to influence local rates of extinction or even local dynamics on the time scales we observe is another question. Metapopulation dynamics are likely important within stream basins at the spatial scales we have considered here, but they may play out over centuries rather than years or decades.

The temporal scale we have defined may be more consistent with finer spatial scales than we have considered. Recent work with the response of fishes following catastrophic defaunation at relatively small spatial scales (10^1 to 10^3 m) shows that numbers of some species may recover very quickly (Detenbeck et al. 1992). For a variety of species, dispersal within streams can be an important element in the local dynamics of recovery (Armstrong et al. 1994; Dunham 1996; Gowan & Fausch 1996; Rieman et al. 1997). It is not clear, however, whether these observations represent dispersal among local populations or the local dynamics of a panmictic group in a patchy environment. Conceivably, local populations and the extinction-colonization dynamic of a metapopulation play out within streams at a smaller scale than we have considered in our work. It will be necessary to resolve the nature of population structuring at even finer scales than we have attempted to understand such results in the context of metapopulation theory.

Finally it is possible, and we think likely, that all of the above are true. Populations within river basins may be hierarchically structured (e.g. Kotliar & Wiens 1990; Wu & Loucks 1995) and temporally and spatially variable. For example, we have recognized dispersal and colonization on both very large (i.e. zoogeographic patterns) and small (river reaches following catastrophic events) spatial and temporal scales. This, combined with the heterogeneity of species and environmental characteristics, suggests a continuum of processes resembling metapopulation dynamics. At some locations, at some scales, with some species, and at some times, extinction and dispersal processes will undoubtedly influence the dynamics and distribution of salmonid populations.

Clearly, far more work is needed to understand the relevant scales of metapopulation processes for salmonids. Emerging patterns indicate the answers will not be simple. Important advances in our understanding of salmonids and metapopulations will require a host of empirical approaches, not only to define patterns, but to identify and quantify important processes and mechanisms as well. Our brief review suggests details necessary for understanding individual species and the complexity of metapopulation processes are generally lacking. What then, are the important issues that must be addressed?

For salmonids, we have shown that patches of suitable habitat and other landscape features can be delineated to consider the spatial structuring of local populations. Our examples of inland salmonids point to the importance of patch size and/or isolation to persistence of some populations (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman, In Press). These patterns potentially reflect metapopulation structuring, but our understanding of processes that actually link local populations (i.e. metapopulation dynamics) remains limited.

Empirical studies of metapopulation dynamics in other animals have relied on time series of extinction and colonization events that occur over relatively short (less than a decade) time periods (e.g. Sjögren-Gulve & Ray 1996). For some inland salmonids at the spatial scale we have considered here it seems likely, however, that extinction and colonization may occur more slowly.

Alternative approaches to understanding the spatial dynamics of inland salmonid populations and new work with anadromous forms are needed.

One possible alternative to direct study of extinction-recolonization dynamics is to indirectly estimate dispersal parameters from patterns of molecular genetic variation (e.g. Neigel 1997). High-resolution genetic markers such as DNA microsatellites offer the potential to define fine-scale relationships among local populations (Fontaine et al. 1997; Spruell et al., In press *this volume*). Direct tracking of individual movements by tagging studies also may contribute important information, but such studies likely underestimate actual levels of dispersal in metapopulations (e.g. Peacock & Smith 1997). Modeling of dispersal processes to identify patterns consistent with observed data (e.g. Karieva et al. 1997; Turchin 1998) also may prove useful, though we are unaware of specific applications to salmonid metapopulations. We caution, however, that with any of these methods precise estimates of migration parameters can be difficult to obtain (Ims & Yoccoz 1996), and that errors in estimation may produce misleading metapopulation and landscape models (e.g. Ruckelshaus et al. 1997).

Another alternative is to focus on dispersal processes and mechanisms, rather than estimation of specific patterns within metapopulations. For salmonids, dispersal appears to be intrinsically constrained by the tendency of fish to imprint on and home to natal habitats to reproduce (Quinn 1993; Cury 1994). Straying does, however, occur, and the ability of fish to disperse to and recognize suitable habitats can have important effects on population dynamics (LePage & Cury 1997). External constraints on among-habitat movement imposed by changes in landscape structure (e.g. Weins 1996; Yahner & Mahan 1997) and the ability of individuals (both adults and juveniles) to detect key habitats (Pulliam & Danielson 1991; Dunning et al. 1992; Schlosser 1994), such as refuge habitats (Northcote 1997), also may have strong effects. Contributions to a better understanding of proximate causes and ecological and evolutionary consequences of habitat selection and dispersal by salmonids (e.g. Jonsson & Jonsson 1993; Smith & Skulason 1996; Willson 1997) are needed.

Given our present limited understanding of salmonid metapopulations, we caution that application of unrealistic models may do more harm than good (see also Doak & Mills 1994; Hanski & Simberloff 1996). We see at least two issues:

First, our own experiences with land management issues and inland salmonids point to a critical problem for conservation; that of resolving the importance of contemporary metapopulation dynamics versus short or long-term changes in suitable habitat (see also Hanski & Simberloff 1996; Harrison & Taylor 1996). In essence, this is a question of how these fishes can track changes in availability of suitable habitat.

If new habitats are made available through protection or active restoration, colonization of that new habitat may lag behind due to the nature of, or constraints on, dispersal. Metapopulation structure implies, to varying degrees, that suitable habitats may not always be occupied. This creates problems for definitions of suitable habitat based on occurrence or standing crop of salmonids (see Dunham & Rieman, In Press). In a metapopulation context unoccupied, but suitable habitat is important. Presently, habitat conservation and restoration are focused on occupied habitat with little knowledge of the importance of succession and patch dynamics (Reeves et al. 1995).

If habitat has been fragmented or lost and the potential for dispersal and recolonization is limited, lagged extinctions in presently occupied habitat also may be anticipated. When rates of local extinction lag behind rates of habitat loss, a "debt of extinction" is incurred (Hanski 1996), so even if further habitat loss is prevented, local extinctions will continue to occur until a new equilibrium between extinction and recolonization is established. To borrow a phrase, many extant local populations may indeed be the "living dead" if extinction debts are a reality. The implication is that conservation of existing habitats alone may not be adequate for the long term conservation of some species.

Second, a metapopulation-based reserve system for one well-studied species likely will not be adequate for many others. It seems highly likely that there are important differences in the life history/dispersal, patch structure, and relevant scales among species. Throughout the Pacific Northwest United States, multiple salmonids co-occur in the subbasins of interest to managers. Even if one could clearly define the metapopulation requirements of each species it seems likely that the resulting management scheme would be extremely complex if not impossible to implement.

We suggest that the primary value of metapopulation theory to conservation of salmonids is not in finding simplifying generalizations or providing minimum reserve designs, but in understanding the relevance of diversity and complexity of these species. The fact that salmonids exhibit complex life histories is a reflection of the diversity of habitats they live in. The interaction between spatial and temporal habitat heterogeneity and life history diversity is central to the concept of "risk spreading" (den Boer 1968; Dunning et al. 1992; Kozakiewicz 1995) in population biology: the idea that naturally diverse populations may have more stable dynamics in the face of environmental changes. Within suitable habitats, increased habitat heterogeneity and risk-spreading may explain why some salmonids are more likely to occur in larger or less isolated patches (Rieman & McIntyre 1995; Dunham et al. 1997; Dunham & Rieman, In Press). At a larger scale, habitat heterogeneity and the structure of landscapes may also be a central component of metapopulation structure, dynamics, and persistence (Wiens 1996; Dunham & Rieman, In Press). In particular, the interaction between dispersal of individuals and landscape characteristics may be critical (Pulliam & Danielson 1991; Schlosser 1991, 1995; Tyler & Rose 1994; Yahner & Mahan 1997).

Considerable work is needed to understand the implications and applications of metapopulation theory for salmonids. We suggest that the most important application, however, will be conceptual. Managers and biologists will likely be more successful in trying to understand and conserve key processes (for example dispersal and linkages between landscapes, life history, phenotypic diversity, and patch size requirements) that likely contribute to persistence whether metapopulations exist or not than in designing minimal networks based on perceived, underlying metapopulation dynamics.

Resumen

1. Metapopulation theory has attracted considerable interest and appears particularly relevant for stream dwelling salmonids. Despite that interest empirical evidence is lacking.

2. Knowledge of life history patterns and our work with three forms, bull trout, Lahontan cutthroat trout, and westslope cutthroat trout, do not support simple generalizations. We suggest the relevance of metapopulation processes will vary with life history, species, landscape, and spatial-temporal scale.

3. More work is needed for specific application of metapopulation theory to conservation of salmonids. Understanding dispersal, the importance of suitable but unoccupied habitat, and the potential for continuing extinctions in non-equilibrium situations are key issues.

4. Conserving key processes (dispersal, the expression of life history diversity, area effects) that contribute to metapopulation persistence will be more useful than designing minimal habitat reserves based on metapopulation theory.

Acknowledgments

A number of people helped with logistical details and with collection of the data summarized with our empirical examples. We recognize the assistance of Ann Abbot, David Bennett, Jim Dunnigan, Debby Myers, Mary Peacock, Robert Schroeter & Gary Vinyard. JBD was supported in part by the U.S.D.A. Forest Service Rocky Mountain Research Station (INT-96089-RJVA), and U.S.D.I. Fish and Wildlife Service, Region 1 (DOI-FW-1960007), with additional support from the Biological Resources Research Center, University of Nevada-Reno. Chris Ray and an anonymous reviewer provided comments helpful in the revision of earlier versions of this paper.

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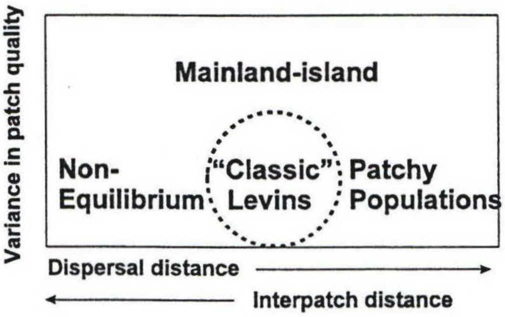
Variance in patch quality
Mainland-island
Non-Equilibrium
"Classic" Levins
Patchy Populations
Dispersal distance
Interpatch distance

Figure 1. Metapopulation structure in relation to variance in patch quality, dispersal distance and interpatch distance (modified from Harrison and Taylor 1996).

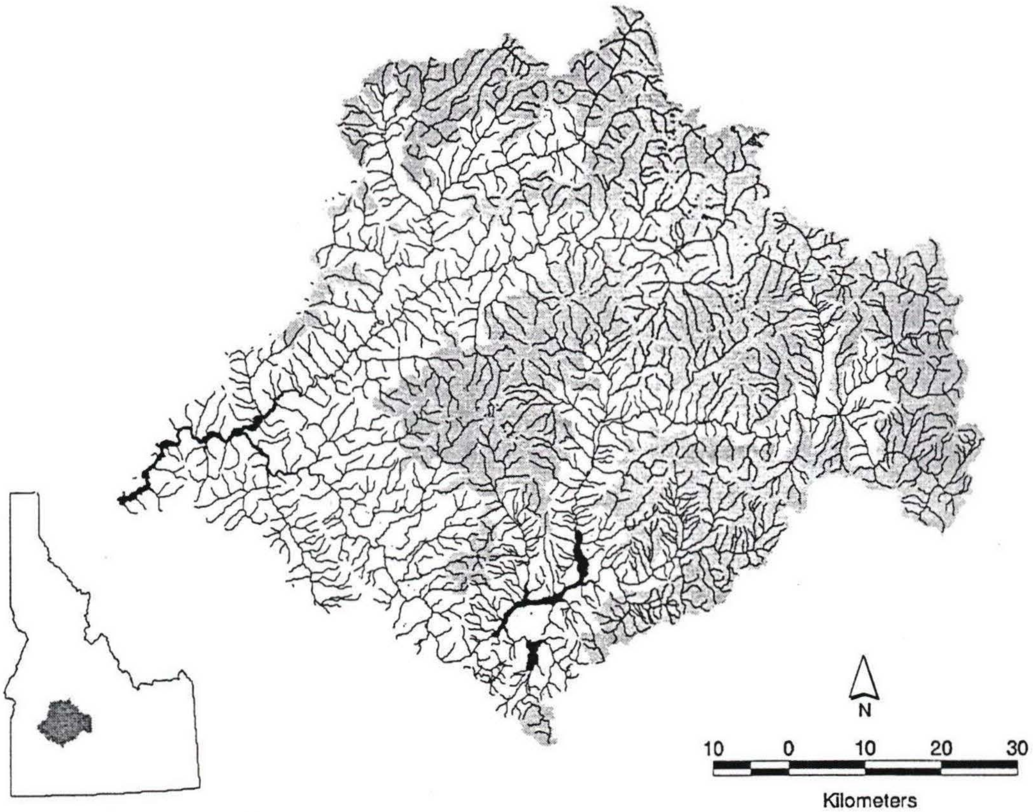

Figure 2. Patches of suitable habitat (shaded catchments) for local populations of bull trout in the Boise River basin, Idaho. Patches were defined from patterns in juvenile bull trout distributions and are assumed to represent the distribution of potential spawning and initial rearing habitats (see Rieman and McIntyre 1995 and Dunham and Rieman In Press).

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Dunham, J., M. Peacock, C. R. Tracy, J. Nielsen, and G. Vinyard. 1999. Assessing extinction risk: integrating genetic information. Conservation Ecology [online] **3**(1): 2. Available from the Internet. URL: http://www.consecol.org/vol3/iss1/art2

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Insight

Assessing Extinction Risk: Integrating Genetic Information

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- Abstract
- Introduction
- Genetic Information and Assessing Extinction Risk
- Caveats and Conclusions
- Responses to this Article
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ABSTRACT

Risks of population extinction have been estimated using a variety of methods incorporating information from different spatial and temporal scales. We briefly consider how several broad classes of extinction risk assessments, including population viability analysis, incidence functions, and ranking methods integrate information on different temporal and spatial scales. In many circumstances, data from surveys of neutral genetic variability within, and among, populations can provide information useful for assessing extinction risk. Patterns of genetic variability resulting from past and present ecological and demographic events, can indicate risks of extinction that are otherwise difficult to infer from ecological and demographic analyses alone. We provide examples of how patterns of neutral genetic variability, both within, and among populations, can be used to corroborate and complement extinction risk assessments.

KEY WORDS: extinction risk, genetic variation, incidence function analysis, population viability analysis, ranking methods, risk assessment, spatial scale, temporal scale.

Published February 16, 1999.

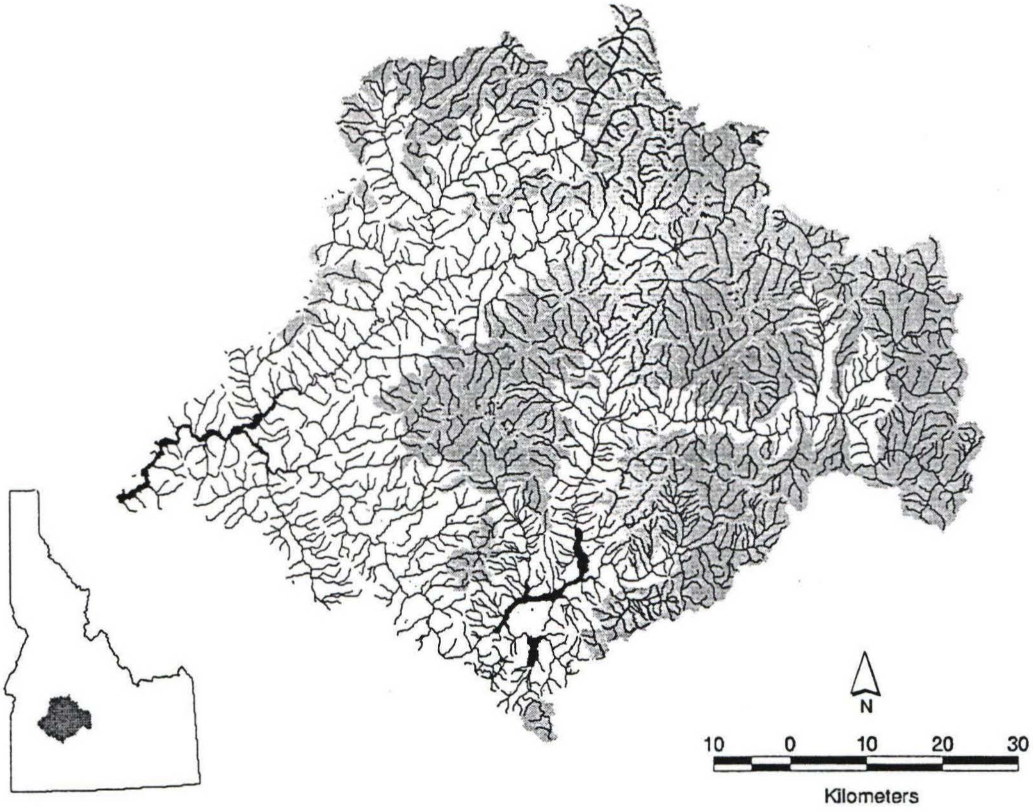

Figure 2. Patches of suitable habitat (shaded catchments) for local populations of bull trout in the Boise River basin, Idaho. Patches were defined from patterns in juvenile bull trout distributions and are assumed to represent the distribution of potential spawning and initial rearing habitats (see Rieman and McIntyre 1995 and Dunham and Rieman In Press).

INTRODUCTION

Assessment of extinction risk among populations is one of the central problems of conservation biology. The development of reliable, yet practical, methods to assess extinction risk is an active and controversial area of investigation (Simberloff 1988, Mace and Lande 1991, Boyce 1992, Burgman et al. 1993, Caughley 1994, Taylor 1995, Mills et al. 1996). Extinction risk is typically assessed in terms of ecological and demographic risk factors (Caughley 1994). Data-intensive methods such as population viability analysis (Gilpin and Soulé 1986, Boyce 1992, Beissinger and Westphal 1998) can be useful when extinction risk of only one or a few populations is in question. When species consist of many populations that may be declining on a local or regional basis, the extinction risk of many local populations must be considered. In such cases, assessments of extinction risk may be obtained by quantitative methods, such as incidence-function analysis (Hanski 1997), or by qualitative ranking methods that incorporate varying types of information (Mace and Lande 1991, Given and Norton 1993, Allendorf et al. 1997). Each method incorporates information on different temporal and spatial scales, and may give potentially different, but complementary, answers to the question of extinction risk (Table 1).

Table 1. Comparison of information from population viability analysis, incidence functions, ranking methods, and genetics.

Method	Basis	Spatial scale	Temporal scale
Population viability analysis	extant populations	one or a few populations	generally > 5 to <50 generations
Incidence functions	extinct and extant populations	many populations	may refer to extinctions on 10^1 to > 10^3 generation time scales, but data are usually from one or two surveys
Ranking methods	extant populations	many populations	highly variable, depending on the type of information used
Genetics	extant populations	many populations	highly variable; may refer to events occurring on a time scale of 10^1 to > 10^3 generations

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Unfortunately, the only objective way to check the validity of extinction risk estimates is to postpone conservation actions and allow more populations to actually go extinct, clearly an unpopular option for imperiled species. Consequently, estimates of extinction risk may be difficult to establish or validate. Comparison of extinction risk estimates from alternative models or methods of assessment can identify important areas of disagreement and for future research, however (Beissinger and Westphal 1998).

GENETIC INFORMATION AND ASSESSING EXTINCTION RISK

In this essay, we briefly consider the potential for patterns of variability in neutral genetic markers to serve as indicators of extinction risk. Although linkages between extinction risk and genetic variability may be obvious to population biologists, opportunities for management applications are only beginning to be fully realized. Our goal in this essay is to focus more attention on the potential utility of genetic variation to serve as a symptom, rather than a cause, of extinction risk (e.g., Caro and Laurenson 1994, Frankham 1995, Lande 1995, Hedrick et al. 1996). A growing literature on the possibilities of linking genetics and ecology in conservation biology (Hastings and Harrison 1994, Milligan et al. 1994, Moritz 1994) suggests that this may be a fruitful approach.

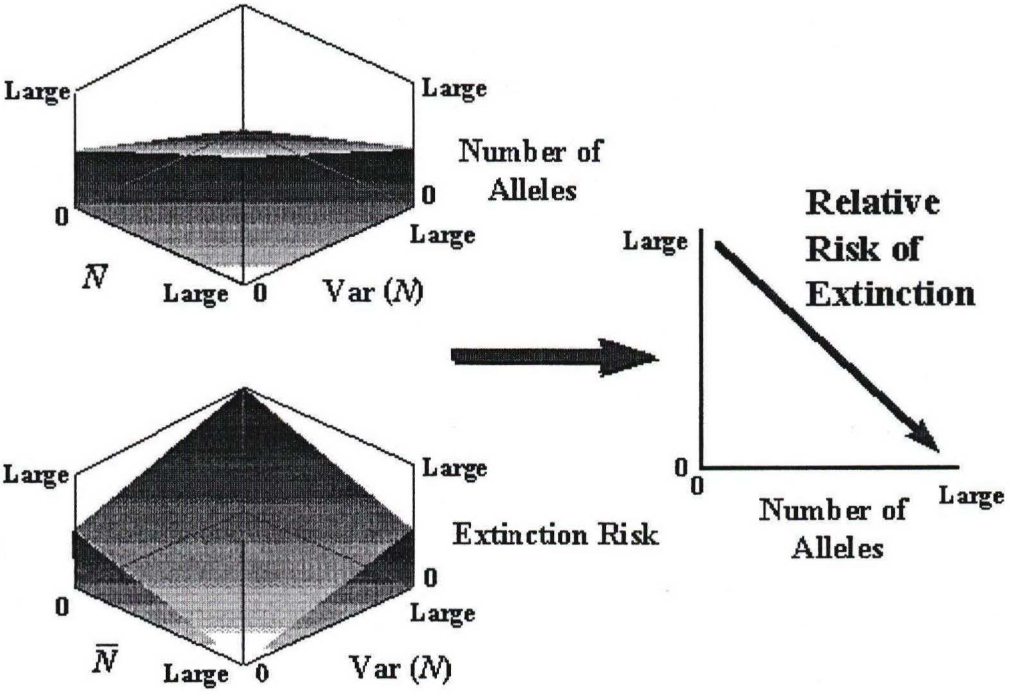
Genetic analysis of population structure typically involves estimating the amount and distribution of genetic variation within and among populations. There are several lines of evidence suggesting that patterns of genetic variation, both within and among populations, may be related to the extinction risk of populations.

Patterns of genetic variation may have a very strong historical component (Slatkin 1985) and, thus, may be a product of very long-term processes. Under many conditions, the effects of historical events can persist for many generations (Avise et al. 1987, Boileau et al. 1992). Historical processes that may decrease genetic variation within populations and increase variation among populations include drift, in small populations, and founder and bottleneck effects (Nei et al. 1975, Boileau et al. 1992, Leberg 1992, DeMarais et al. 1993, Frankham 1996, Richards and Leberg 1996). Extinction-recolonization dynamics also may decrease differentiation within and among local populations, particularly when population turnover rates are high (Hedrick 1996, Hedrick and Gilpin 1996).

This linkage between population size and variability and genetic variation suggests that levels of within- and among-population variability may reflect the relative risk of extinction among populations (Fig. 1). In theory, extinction risk may be inversely related to population size and positively related to variability in population size (e.g., Shaffer 1981, Goodman 1987, Lande 1993; see Fig. 1). This relationship has been suggested for some empirical data, but generalization of this pattern remains controversial (see Pimm et al. 1988, Schoener and Spiller 1992, Tracy and George 1992) and should be regarded as a working hypothesis.

If our characterization of relationships between genetic variation and extinction risk is correct (Fig. 1), then levels of within-population genetic variation and estimates of extinction risk may be inversely related. A recent review of patterns of within-population variability across a wide range of taxa (Frankham 1996) supports this generalization. Frankham found direct correlations between levels of within-population genetic variation and measures of population size, and significantly lower levels of genetic variation in endangered vs. nonendangered species.

Fig. 1. Hypothesized relationships between average population size (*N*), variability in population size, extinction risk, and within-population genetic variability (number of alleles per locus: Low, Moderate, High). Note that there are several alternative measures of within-population genetic variability (Leberg 1992).

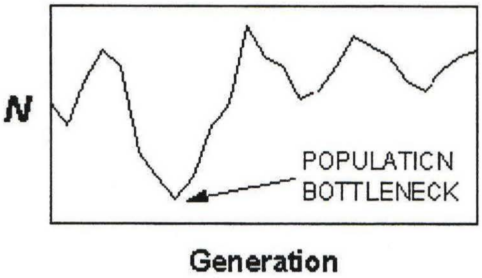


At the among-population scale, recent empirical study of a butterfly metapopulation (Saccheri et al. 1998) similarly found a direct correlation between the extinction risk of local populations and heterozygosity. Saccheri et al. also provided circumstantial evidence to implicate inbreeding in populations with reduced heterozygosity as a mechanism contributing to local extinctions. In this example, reduced genetic variability may be a symptom, as well as a cause, of local extinctions.

Certainly, discrepancies from hypothesized patterns in Fig. 1 are expected. Such discrepancies may reveal instances in which demographic or ecological events have not been appropriately incorporated into assessments of extinction risk, or cases in which genetic variability is a poor indicator of risk (see *Caveats and conclusions*). Examples of potential discrepancies will be described.

First, if an extinction risk assessment using ecological or demographic methods predicts a high probability of persistence for a particular population, but levels of observed within-population genetic variability are low, then historical (or infrequent) events not captured in the assessment may need to be considered. Low levels of within-population genetic variation may indicate the occurrence of environmental catastrophes or other events that have caused population bottleneck or founder events not detectable in short-term demographic or ecological surveys (e.g., Fig. 2). Unless populations are tracked for many generations, patterns of genetic variation may be the only way to reconstruct or infer the occurrence of catastrophic events that may be crucial in terms of extinction risk (Mangel and Tier 1994, Young 1994, Foley 1996).

Fig. 2. Population time series with a single population bottleneck shown (N = population size). Estimates of demographic parameters based on time series data collected after the bottleneck event may underestimate variability in population growth rates and extinction risk. The signature of such events may be present in patterns of genetic variability within populations, however.



A second discrepancy may arise when ecological or demographic methods predict a low probability of persistence for a population, but within-population levels of variability are relatively high. A potential example is provided by bull trout (*Salvelinus confluentus*) populations in streams of the Lake Pend Oreille basin, Idaho, United States. Extinction risk assessments based on time series of redd (gravel pits excavated by female trout for egg deposition) counts suggested that bull trout populations in streams with consistently low redd counts were likely to go extinct within the next 100 years (Rieman and McIntyre 1993). Recent genetic analyses (Spruell et al. 1999) revealed, however, that levels of genetic variability within populations were not related to population size as indexed by redd counts. This finding has motivated the development of more realistic demographic models (D. Lee and B. Rieman, U.S.D.A. Forest Service Rocky Mountain Research Station, *personal communication*), increased scrutiny of redd counts as an index of population size, and re-evaluation of the population structure of bull trout in general (Dunham and Rieman 1999).

A similar example can be found for pika (*Ochotona princeps*). Extinction and recolonization dynamics of habitat patches in a pika metapopulation suggested loss and coalescence of genetic variation (Gilpin 1991, Smith and Gilpin 1997). However, analysis of multilocus DNA fingerprinting data revealed high levels of heterozygosity (Peacock and Smith 1997). Mark-recapture data, combined with genetic data, revealed an important component of gene flow, among-patch movement in between extinction events, not captured by extinction-recolonization dynamics. The additional component of juvenile dispersal to occupied patches appears to be important to patch occupancy rates, patch persistence, and maintenance of genetic variation (Peacock and Smith 1997).

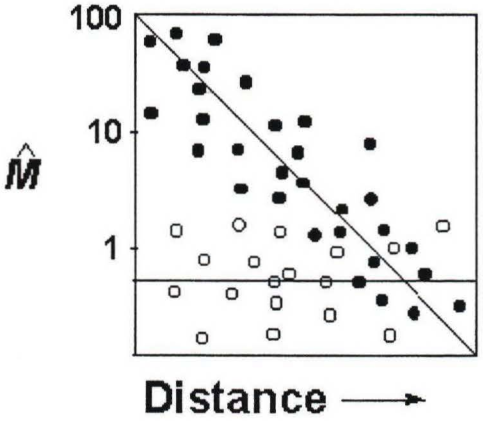
As with patterns of within-population variability, patterns of genetic variation among populations may provide useful information about extinction risk. Patterns of genetic variation among populations are often used to infer levels of migration or gene flow. Migration rates from genetic data are typically derived from F statistics or analogous measures of among-population genetic variability (Neigel 1997). This approach assumes a migration-drift equilibrium, which may not be valid in many situations, especially for organisms prone to local population bottlenecks or founder events (Boileau et al. 1992, Slatkin 1993). Species with such dynamics may pose difficulties in terms of estimating demographic parameters (e.g., dispersal), but patterns of genetic differentiation among populations may be useful for identifying populations at risk of extinction.

When populations become subdivided by habitat fragmentation, founder events, or similar biogeographic or ecological processes, among-population genetic differentiation will theoretically approach a migration-drift equilibrium at a rate determined by time since divergence, migration rate, and population size (Boileau et al. 1992). The approach of populations to a migration-drift equilibrium can take many generations for some species, particularly when founder events or genetic bottlenecks are followed by rapid population increases to a relatively large size (Boileau et al. 1992).

Slatkin (1993) proposed statistical methods for detecting nonequilibrium genetic differentiation in natural populations. When genetic differentiation is a function of geographic distance between local populations, pairwise estimates of gene flow should be inversely related to interpopulation distances at equilibrium (Slatkin 1993). Low estimates of gene flow, coupled with lack of isolation by distance, may indicate nonequilibrium genetic differentiation due to bottleneck and founder effects, or extreme isolation (Boileau et al. 1992, Slatkin 1993, Britten et al. 1995). The result is that genetic differentiation may be overestimated and gene flow underestimated.

If populations experiencing isolation due to habitat fragmentation or frequent bottleneck and founder events are at greater risk of extinction, then the isolation by distance method (Slatkin 1993) may be used to identify at-risk populations (Fig. 3). Pairwise estimates of migration should be an inverse function of the geographic distance separating populations at equilibrium (Slatkin 1993; see Fig. 2). Although not yet described for any data sets that are familiar to us, it may be that unique functions (e.g., curvilinear or piecewise) may be necessary to describe isolation by distance when dispersal is not a linear function of geographic distance. For simplicity in this discussion, we assume a linear relationship (Fig. 3).

Fig. 3. Linear relationships between the estimated pairwise number of migrants per generation ($\hat{M}$) and geographic distance (log scale). Solid circles represent populations with equilibrium divergence and open circles represent nonequilibrium genetic divergence.



A species may consist of both equilibrium and nonequilibrium local populations (Hellberg 1995, Green et al. 1996; see Fig. 3). For example, patterns of nonequilibrium divergence suggesting low migration rates due to isolation or severe constrictions in population size (e.g., open circles in Fig. 3) may indicate isolation by fragmentation, or perhaps the genetic legacy of a catastrophic disturbance. Similar patterns of nonequilibrium divergence have been linked to long-term climate change and fragmentation of aquatic habitats for southern spotted frog populations (*Rana pretiosa,* Green et al. 1996). In the case of group of pocket gopher (*Thomonys bottae*) populations in central California, low estimates of gene flow and nonequilibrium divergence may have resulted from extreme isolation (Slatkin 1993; see also Britten et al. 1995). For a second group of pocket gopher populations, lack of isolation by distance and high estimates of gene flow suggested an alternative pattern of transient disequilibrium produced by recent colonization events (Slatkin 1993).

CAVEATS AND CONCLUSIONS

The extent to which patterns of genetic variability reflect extinction risk will depend upon how alternative demographic and ecological conditions are related to extinction risk. For example, we suggest that patterns of within-population genetic variability may indicate the occurrence of past catastrophes, events that may cause local extinctions. Although some theoretical work suggests that conventional assumptions about extinction risk from catastrophes may be exaggerated (Lande 1993), empirical evidence from natural populations (e.g., Young 1994, Foley 1996) suggests that catastrophes may be of sufficient magnitude and frequency to pose substantial risks to the persistence of local populations (see also Mangel and Tier 1994).

It is also likely that some species with limited within-population variability, or nonequilibrium population structure, may be well adapted to persist in the face of extreme isolation or small population size. This may be the case for species that inhabit naturally isolated, but relatively stable habitats.

Finally, past threats to populations (e.g., harvesting, land use, disease, etc.) may no longer be relevant to present or future extinction risk. This possibility must be considered carefully because information on past extinctions may not be useful in contemporary risk assessments and vice versa.

Different methods and approaches to estimating the risk of extinction integrate information on a variety of spatial and temporal scales (Table 1). For example, incidence functions (Hanski 1997) incorporate information on broad-scale patterns of local extinctions that may have occurred in the recent past, or during historical events that occurred decades, hundreds, or even thousands of years (or generations) ago. Furthermore, incidence functions often provide only a "snapshot" or static picture of species' occurrence. For many species, it may be difficult to study temporal patterns of occurrence, because extinction and recolonization of habitats may occur on very long time scales (e.g., Dunham and Rieman 1999).

Methods of assessment based on detailed demographic data from extant populations, such as population viability analysis, are generally limited to one or a few local populations and relatively short time scales, which may not represent the regional dynamics of a species (Middleton and Nisbet 1997). Furthermore, large data requirements and model uncertainty may limit the utility of demographic viability models to produce reliable extinction risk estimates (Mills et al. 1996, Beissinger and Westphal 1998).

Patterns of genetic variability are based on extant populations, and should incorporate information from a large number of populations. This is because processes occurring on a variety of spatial and temporal scales may influence patterns of genetic variability. There are no simple or general guidelines for exactly how genetic, demographic, and ecological information should be integrated. However, the examples presented here illustrate that the complexity of long-term population dynamics may not be revealed using any single approach. Here, we emphasize the potential of genetic information to complement inferences from demographic and ecological approaches and encourage managers to carefully consider the evidence from each of these diverse sources of information in extinction risk assessments.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a comment, follow this link. To read comments already accepted, follow this link.

Acknowledgments:

We thank C. Ray and two anonymous reviewers for constructive comments on earlier versions of this manuscript. J. B. Dunham and M. M. Peacock were supported, in part, by the U.S.D.A. Forest Service Rocky Mountain (formerly Intermountain) Research Station (INT-96089-RJVA), and U.S. Fish and Wildlife Service, Region 1 (DOI-FW-1960007), with additional support from the Biological Resources Research Center, University of Nevada-Reno. J. L. Nielsen acknowledges the support of the U.S.D.A. Forest Service Pacific Southwest Research Station.

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